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A Monograph of the Nearctic Plagiochilaceae

Part III. Sectio Contiguae to Conclusion.*

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Duke University, Durham[1]

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Sectio VIII. Contiguae Carl

Plants sparsely branched, the branches (in our species) on weak shoots usually monopodial, intercalary, diffuse, but on *mature shoots often* 2-4 × *pseudodichotomously furcate* and terminal in origin. *Plants green* becoming slightly brownish with age in some species, *usually dull,* medium sized (2-3.3 mm wide) to robust (3.5-5 mm wide). Stem with cortex 2-3 (-4) stratose, firm, of thick-walled, elongate cells. Leaves varying from contiguous to weakly imbricate, laterally patent when moist, firm and usually relatively opaque, broadly to narrowly *ovate or ovate-falcate,* the antical margin nearly straight to concave normally; the *postical margin strongly to moderately ampliate* (at least just above base), the widest point just above the leaf-base; leaf-width varying from *ca.* 1.2 to 2.2 *the leaf-length;* line of insertion of the leaves elongate, the leaves rather *long-decurrent dorsally,* but relatively *short-decurrent* (*ca.* 0.2 × the merophyte length) *postically,* the decurrent strip *not or narrowly and obscurely reflexed, edentate,* not forming a water sac or prominent crista; leaves distinctly dentate to spinose-dentate (rarely nearly edentate in *P. aspleniformis* and *dubia*), usu-

* Two previous sections of this work have appeared in *The American Midland Naturalist,* **62**(1):1-166; **62**(2):257-395. This is the terminal section and contains the references for the entire monograph.

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ally with 1-2 teeth near apex of antical margin (the edentate portion of antical margin more or less reflexed; the cnemis moderately distinct to well-defined), with 2-several teeth at the often subtruncate apex, and with 2-6 teeth on the postical margin. *Cells medium sized, ca.* 18-24 μ wide medially, with small or minute to distinctly bulging trigones; oil-bodies formed of protuberant, coarse globules, appearing coarsely papillose or segmented, mostly 3-6 per cell, but rarely to 11 per cell, moderately large (to 5 x 10 μ). *Underleaves vestigial,* of 1-several short cilia. Asexual reproduction *usually present, by leafy propagula* formed on the postical face (more rarely, and to a lesser degree, also on the antical face) of the leaf.

Female plants (where known) with a short, included perianth, obdeltoid to obcuneate in lateral view, the ciliate mouth nearly or quite as wide as the dorsal keel is long; *dorsal and ventral keels subequal in length* (at least when perianth is juvenile); dorsal keel usually (always?) winged, at least at base.

The present section is closely allied to the Sectio Yokogurenses and the Sectio Hypnoides. The first of these, including only *P. yokogurensis,* differs from the present group of species in the more copiously pseudodichotomous branching, and in the caducous distal halves of the leaves. The second of these groups, Sectio Hypnoides, is separated from the present complex by the cristate postical leaf-bases, which are normally strongly reflexed and often more or less dentate, by the denser leaves, and by the development of lamellate underleaves.

These three sections are similar in the essentially ovate or ovate-falcate leaves, in the ability of their species to produce leafy propagula, as well as in the basically similar oil-bodies of all species concerned, in the laterally spreading (never postically secund) leaves, in the limited number of teeth (usually less than 15-20) the leaves are able to produce, in the basically similar cell-size of most of the species, in the lack of a basal vitta, and in the apparent inability of their species to produce sporophytes. Of these three sections, the present one appears to be by far the least specialized (and possibly stands ancestral to the two others). The Sectio Yokogurenses appears to be derived by the development of more fragile leaves, which develop the ability to fragment; the Sectio Hypnoides and Sectio Crispatae appear to have been derived by the greater elaboration of the postical base and the greater decurrence of the postical margins. Some members of the Hypnoides and Crispatae are transitional and thus make a separation difficult to maintain. However, all the Contiguae have minute, often ephemeral underleaves, while the Hypnoides and Crispatae mostly possess large and distinct underleaves. These two sections, furthermore, have much more closely imbricate leaves than the Contiguae.

Branching in the Contiguae is quite diverse and needs to be intensively studied. It is clear that in some species (*P. dubia, P. virginica, P. floridana* and *P. aspleniformis*) there are frequent or at least occasional "pseudodichotomous" branches, *i.e.,* terminal branches where the main axis is laterally displaced so

that the main shoot appears once or repeatedly furcate (see Fig. 55A:1, *P. floridana;* Fig. 56:3, *P. aspleniformis*), although branches may arise largely in an axillary position, from older shoot sectors, as intercalary branches. In the presence of terminal branches the Contiguae approach the Yokogurenses, where pseudodichotomous, furcate branching is common, although axillary branches are also common in the one species of that section studied. The Contiguae also approach, in this respect, the Parallelae, which are characterized by a regular furcate, decompound branching (see Schuster 1959a, Fig. 41:6, *P. diffusa*). These three sections are further characterized by having perianths with the mouth truncate at nearly right angles to the axis, or with the mouth only slightly oblique — thus with the postical keel nearly or quite as long as the antical; and by the ability to develop propagula. The first of these last two characteristics is shared with several preceding sections (Choachinae, Bidentes, Asplenioides, Zonatae), which, however, never or only abnormally produce terminal branches. The ability to produce propagula is shared with the Hypnoides and Crispatae, sections in which the perianth-mouth is typically strongly obliquely terminated with an abbreviated postical keel.

PLAGIOCHILA VIRGINICA Evans
Figs. 43-48

Plagiochila virginica Evans, *in* Millspaugh, Flora of West Virginia 497, 1892; Evans, Bot. Gaz. 21:190, 1896, in part (West Virginia plants only).

Plants growing in intertwined patches, the rhizomatous stems often ± leafy, creeping, giving rise to distant to closely approximated, simple or on mature shoots commonly dichotomous aerial stems, *plants green to deep green, dull, without brownish pigmentation.* Leafy shoots when mature (2.5) 2.75-3.2 mm wide, occasionally 3.5-3.8 (4.0-4.8) mm wide and *ca.* 1.3-2.0 cm long, occasionally to 3 cm long. Stems from a minimum of *ca.* 150-165 to 190-250 μ, occasionally 400-430 μ wide; with cortex (type) green to brownish, scarcely thick-walled (bistratose); on robust plants (stem to 430μ wide) cortex strongly brownish, 2-3 stratose, the cortical cells ± tangentially flattened, thick-walled, brownish, (13) 14-16.5 μ wide; medulla varying from 6-7 to 12-14 cells high depending on robustness of stem, of ± thin-walled, pellucid cells, (18) 21-27 (30) μ in diameter. Branches on weak plants exclusively monopodial and intercalary, few or none from leafy aerial shoots; on robust ♀ plants aerial shoots commonly once or twice furcate, the branches terminal in origin. Rhizoids infrequent, except at bases of aerial stems, but occasionally on some aerial stems, which may become decumbent and rhizoidous. Leaves *approximate to moderately imbricate, widely spreading* (*ca.* 60-80°), essentially obliquely, asymmetrically, *rather broadly ovate,* their line of insertion slightly arched acroscopically, but the *postical base exceedingly short-decurrent* (*the stem consequently usually very considerably exposed, in postical aspect*); antical base moderately decurrent; leaves *ca.* 1050-1100 (1250-1400) μ wide x 1500-1650 (1700)μ long, occasionally to 1500-1600 μ wide x 1900-2050 μ long (1.25-1.45 [1.6] × *as long as wide*), widest *shortly above the base;* postical margin arched, (*but often only moderately dilated basally*), the antical margin nearly

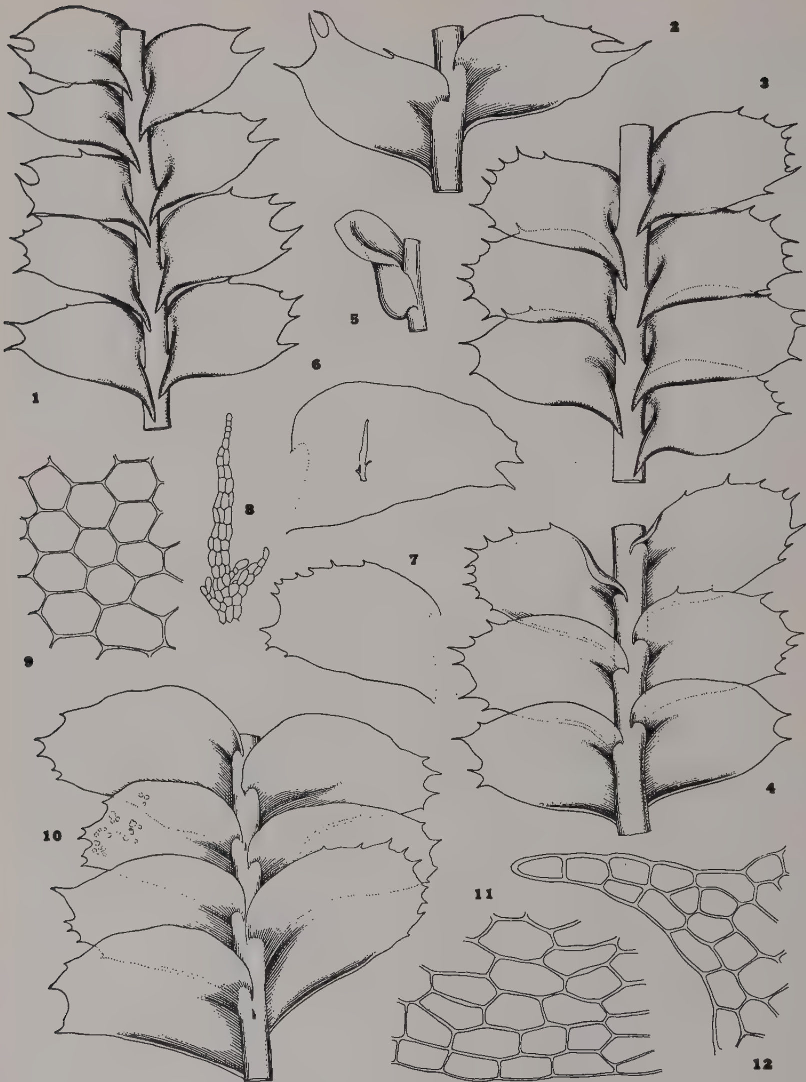

Fig. 43.—*Plagiochila virginica* Evs.. 1. Weak shoot, antical aspect (x *ca.* 20); 2. Sector of atypical, weak shoot, postical aspect (x 16); 3-4. Sectors of most robust extreme seen of type plants, antical and postical aspects (3, x 19; 4, x 15); 5. Atypical male bract from rudimentary androecium (x *ca.* 8); 6. Large leaf, and to same scale, associated underleaf (x 16); 7. Medium-sized leaf (x 16); 8. Underleaf (x 58); 9. Median cells (x 175); 10. Postical aspect of shoot-sector, the propagula-initials drawn in on one leaf only (x 16); 11. Cells of postical leaf base (x 180); 12. Tooth near leaf-apex (x 175). (Figs. 1-4 from type of *P. virginica;* 5-12, from plants collected at Island Home, e. of Knoxville, Tenn., *Sharp* 34339.)

straight or with basal $^1/_4$ to $^1/_3$ (rarely $^1/_2$) reflexed (thus often appearing concave in profile), the distal portion straight to slightly convex; *postical base not or scarcely, narrowly erect, not usually reflexed;* antical margin entire, except near apex (where occasionally with 1-2 teeth); postical margin usually subentire or entire, except on distal ½ to ¼ (where with 1-5 small, scarcely spinose teeth); apex with 2-5 (6) obtuse to spinose teeth, occasionally with two larger and evidently lobe-like; *teeth small and short,* usually 2-3 cells high and 1-2 cells wide at base to 4-5 cells long and 3-5 cells wide at base, the apex often of two single, nearly isodiametric cells in a row; the *margin as a whole with usually* 4-10 *teeth,* but on juvenile leaves often only the two apical, lobe-like teeth discrete. Cells slightly (type) to distinctly collenchymatous, the apical from *ca.* 18-20 μ (type) to 20-24 (rarely 24-28) μ; the marginal cells along apical half of postical margin *ca.* 16-19 (21) μ; the *median cells ca.* (21) 23-25 (26) x 23-32 (35) μ; basal cells not or scarcely evenly thick-walled; cells at postical base 1.3-2.5 × as long as wide, *ca.* (12) 14-17 x 21-26 (30-38) μ up to 18-20 x 32-40 μ, with longitudinal walls not very prominently thick-walled; oil-bodies 8-12 per cell in most median cells, mostly 2 x 4.5 μ to 2.5 x 5 μ, but occasionally to 3 x 7 μ or even 2-3 x 8-9 μ, *formed of coarse segments* (usually a row of 2-5 globules forming an oil-body, sometimes with the median part of the oil-body of 2 rows of segments), each *ca.* 1.8-2.2 μ in diameter; in a few cells oil-bodies largely homogeneous, or 2-3 segmented, and only 2.5-4 μ in diameter (then smaller than chloroplasts); chloroplasts normally *ca.* 4-5.5 μ in longer diameter. *Underleaves appearing absent* (reduced to stalked or unstalked slime-papillae) *or minute* (of 1-2, occasionally 3-5, ciliary segments terminated by slime papillae), occasionally lanceolate. *Asexual reproduction by means of propagula from the postical leaf-surface.*

Dioecious. Usually sterile. Male plants very rare; the bracts (perhaps not fully developed) with concave, erect base, somewhat flaring apex, the margins entire or ending in a blunt tooth. Female plants rarely developed, usually more robust (to 4.5-5 mm wide x 2.5-3.5 cm long) and occasionally pseudodichotomously furcate. Bracts ovate-rectangulate, the strongly reflexed antical margin nearly straight, the *apex commonly broadly subtruncate,* the postical margin rather strongly dilated above base but nearly straight distally, varying from 1400 μ long x 1000-1150 μ wide to 1500 μ long x 1200-1225 μ wide (averaging slightly smaller than robust leaves), undulate on the postical margin, *strongly and irregularly serrate-dentate to spinose-dentate,* the postical margin with 5-7 or 10-14 coarse and irregular teeth, the truncate apex with 2-4 irregular, coarse teeth, the *antical margin edentate* or with a single preapical tooth. Perianth (juvenile only known) obdeltoid in lateral profile, compressed laterally, *antical keel not or hardly longer than postical,* the antical keel *in basal half with a weak lamellate carina* that is edentate, the rounded-truncate mouth coarsely but not closely dentate, the *teeth not spinose* (terminal cells mostly 13-15

x 20-23 μ, not strongly attenuate; subterminal cells nearly or quite isodiametric), the teeth broad-based, commonly 3-6 cells wide at base x (4) 5-10 cells long, *the apex uniseriate for a length of only* 1-2 *cells.*

Type.—Beaver Spring, near Mercer, West Virginia (*F. Millspaugh* 1550), 1890; type in Yale Herbarium!; cotype in Herbarium of NYBG!

The preceding description is based in part on sterile plants of the type (a mod. *parvifolia-viridis-leptoderma*), from which the minimal measurements are derived, in part from more robust plants, more typical of the species, of *Schuster* 37625. From this the gynoecial data are derived, as well as the maximal measurements given.

Distribution.—Imperfectly known, but apparently ranging in the upper edge of the Piedmont and lower elevations of the Appalachian Plateau from Virginia and West Virginia to northern Georgia, and northeastern Mississippi at elevations of usually 1800-3000 ft.; southward to the juncture of the Interior Plateau region and the inner Coastal Plain, in N.E. Mississippi (there at an elevation below 750 ft.!).

WEST VIRGINIA: In Limestone cave, Beaver Springs, near Mercer, May 25, 1892 (*C. F. Millspaugh* 1550! *type*), *Isotype* examined in NYBG! VIRGINIA: Sinking Creek at base of Salt Pond Mountain; on vertical shaded limestone, rocky outcrop near water, at spring outlet to Harvey's Cave (*Patterson* 1426!); deep gorge of Big Devil's Stairs, Shenandoah Ntl. Park, Rappahannock Co., on noncalcareous rocks (*Patterson* 2205!); The Cascades near Hot Springs, Bath Co., on limestone (*Patterson* 1448!); NE. side of Bent Mt., on rock in woods, 2500 ft., Roanoke Co. (*Patterson and Sharp R*-311!); base of gorge at the Pinnacles, Dan R. Gorge, Patrick Co. (*Patterson and Anderson* 1375 p. p., with *Frullania squarrosa*); Cascades, 2900 ft. and lower, Little Stony Cr. near Mt. Lake, Giles Co. (*Schuster* 40202, 40236); Limestone cliff 3 mi. SE. of Bluegrass, Highlands Co. (*Patterson* 2441!; transitional to var. *caroliniana*); Marty Branch, Dismal R., Buchanan Co., on Gladeville Sandstone (*Patterson* 2584!; somewhat atypical, the subapical cells often only 12-16 μ; postical cells elongated, their longitudinal walls $\pm$ thick-walled; a somewhat leptodermous var. *caroliniana*?). Also reported from Giles and Buchanan Cos. (Patterson, 1955). The previous report of this species from Virginia (in Patterson, 1950) is incorrect and is referable to *P. yokogurensis* subsp. *fragilifolia.* NORTH CAROLINA: Linville Caverns, near outlet of spring, moist limestone (associated, nearby, with *Plagiochasma wrightii* and the ferns *Camptosorus rhizophyllus* and *Asplenium cryptolepis*), on Rte. 221, McDowell Co. (*Schuster* 29058, 28814); same locality, but on exposed, dry, calcareous cliff, associated with *Frullania squarrosa* and *Radula complanata,* and the xerophytic ferns, *Asplenium cryptolepis* and *Polypodium polypodioides* var. *michauxiana* (*Schuster* 29043, 28809, 29060); upper falls, Whitewater R., Jackson Co. (*Anderson* 8747! *Schuster* 40567); Rocks in canyon of lower course of Dark Ridge Creek, near Balsam (*Andrews* 274! in herb. Y as *P. ludoviciana;* a delicate, green phase with moderate to barely bulging trigones); intermittently damp rocks by waterfall, above Linville Caverns, McDowell Co. (*Schuster* 40351, 40367, 40372; with *Anomodon, Radula complanata, R. andicola, Metzgeria conjugata, Lejeunea laetevirens*). Calcareous rock-face above falls of Crow Creek, Cullasaja Valley between Highlands and Franklin, Macon Co. (*Schuster* 40856; a small, virtually unbranched xeromorphic sun phase); on sandstone boulder, gorge of Pacolet River, near Tryon, Polk Co. (*Patterson* 2848!, 2845!; the former a

"normal" phase with small trigones, the latter a more brownish, xeromorphic phase approaching var. *caroliniana*). SOUTH CAROLINA: West branch of Estatoe River, in ravine, Pickens Co. (*Schuster* 37625, 37651b, 37625a, 37620b, 37669a, 37624a; the robust extreme of the species, freely producing gynoecia and propagula; in part approaching var. *caroliniana*); open S. end of gorge of Estatoe R., N. Pickens Co. (*Schuster* 37690a); transitional between the species and var. *caroliniana* is the collection from Whitewater R. Gorge, above Jocassee, Oconee Co. (*Schuster* 25108). TENNESSEE: Little America, near Island Home, Knox Co. (*Sharp* 34339, *male plants*); siliceous rock, Hickory Creek below Jellico, Campbell Co. (*Sharp* 3643; fragmentary, a mod. *parvifolia-subintegrifolia,* with median cells only 18-21 μ; possibly mesodermous phase of var. *caroliniana*); calcareous rock, Ladd's Cove, Bottle Creek, Marion Co. (*Sharp* 34956); calcareous bluff, near Jasper, Marion Co. (*Sharp* 34927 p. p. with *Radula complanata*); Bluff, left prong of Greenbrier, above 3000 ft., Sevier Co. (*Sharp* 3873; mixed with *P. sharpii* subsp. *sharpii;* cells small, the median 20-24 μ wide; postical leaf-base with longitudinal cell-walls thick; approaching var *caroliniana*). GEORGIA: Unicoi Gap, White Co.., 2968 ft. (*Schuster* 25761, 25761a, 25761b). MISSISSIPPI: Tishomingo State Park, Tishomingo Co., *ca.* 750 ft., on subcalcareous sandstone (*Schuster* 19738, p. min. p., among *Frullania asagrayana* cf. *tamarisci*).

As is developed elsewhere, the report of this species from Washington, D.C. (Evans, 1896) is based on misdetermination of *P. yokogurensis* subsp. *fragilifolia.*

Ecology.—*P. virginica* appears to be typically a species of damp to dry limestone or sandstone ledges or cliffs. Although not uniformly associated with limestone ledges, the association is a marked one when one considers that in the Southern Appalachians calcareous outcrops are rare and local, yet more than half of the collections of *P. virginica* seen are cited as from calcareous rocks.

On calcareous boulders and cliffs, in partially exposed sites, common associates are *Radula complanata, R. andicola, Frullania squarrosa, F. plana, Porella platyphylla* and *platyphylloidea,* and with accumulation of a little soil, *Reboulia hemispherica,* as well as the mosses *Anomodon minor, A. attenuatus,* and *A. rostratus.* The *Plagiochila,* and associated bryophytes form dense mats, intermittently dry, in which such xerophytic ferns as *Asplenium resiliens* and *Polypodium polypodioides* undergo ecesis (in *Schuster* 28809, 29043, 29060; Linville Caverns, N.C.). Similarly, on calcareous bluffs (*Sharp* 34927; near Jasper, Marion Co.) the liverwort *Radula complanata* and mosses *Anomodon attenuatus, A. rostratus* and *Taxiphyllum geophyllum* are associated. At both of these sites, where conditions verging on the xeric pertain, the *Plagiochila* occurred as a large-celled, nearly leptodermous phase. This is the phase from which the species was described, from limestone at the entrance to a cave.

P. virginica also occurs on large and medium-sized, noncalcareous boulders, lying in relatively open Oak-Hickory forest (as at Unicoi Gap, Georgia; *Schuster* 25761 *and* 25761a, b). The associated hepatics at this site were *Frullania plana, Porella platyphylloidea, Metzgeria crassipilis,* and *Radula complanata.* The plants, from this site, from an unusually xeric habitat, possessed slightly to moderately bulging tri-

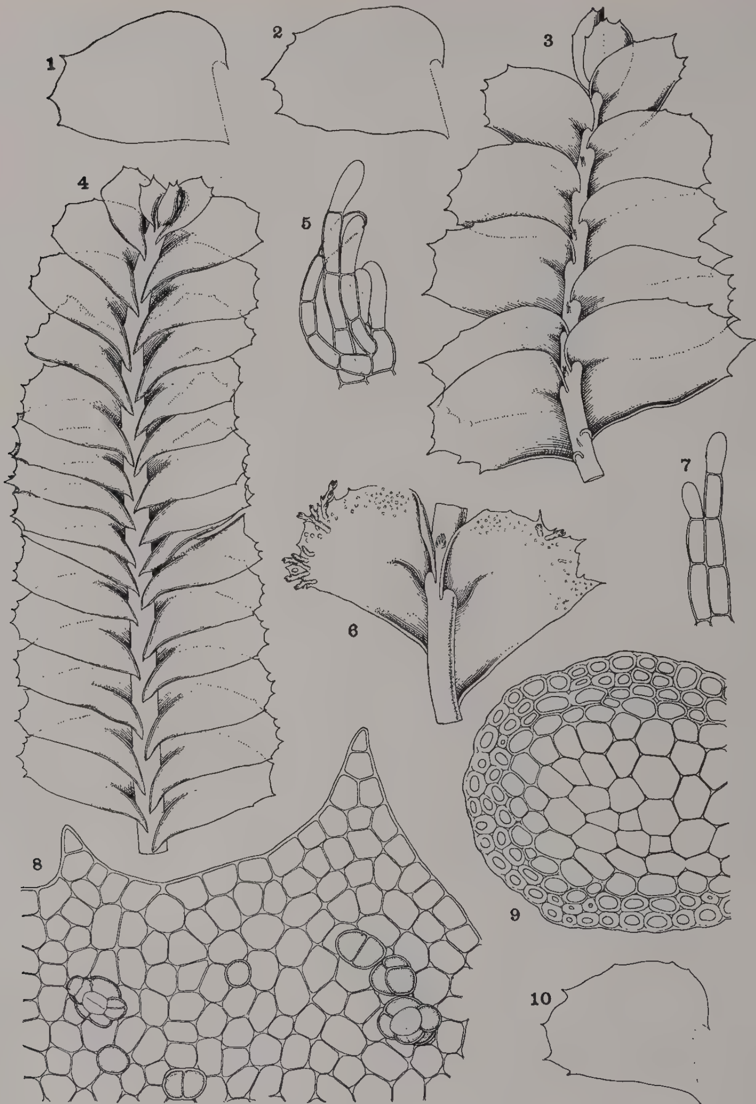

Fig. 44.—*Plagiochila virginica* Evs., typical. 1-2. Leaves (x 16); 3. Large shoot, postical aspect (x 13.5); 4. Shoot, antical aspect (x 12); 5. Relatively large underleaf (x 220); 6. Postical aspect of shoot-sector with propagula (x 13); 7. Underleaf (x 280); 8. Cells of leaf-apex, with young propagula (x 215); 9. Stem cross-section (x 175); 10. Leaf (x 13). (Figs. 1-5, 7-10, from plants collected at Unicoi Gap, Georgia, *Schuster;* for oil-bodies see Fig. 60:8; fig. 6, Linville Caverns, N.C., *Schuster* 29043.)

gones, but lacked the confluent trigones of the postical leaf-base. Other collections from "on rocks in woods" and from "sandstone boulders in woods" have been seen. The species is also common on boulders and ledges in rich Oak-Hickory forest at Tishomingo State Park, Mississippi (*Schuster* 19738), over sandstone rock-walls, associated with xerophytes such as *Frullania asagrayana,* cf. *tamarisci, Porella pinnata, Polypodium polypodioides,* etc. Such xerophytic and meso-xerophytic occurrences appear to be much commoner than the few cases where the species has been found on "moist rocks, at base of gorge" or "moist limestone cliffs."

The marked frequency on, if not obligate restriction to, limestone rocks, and the ability to tolerate relatively xeric conditions are the two most marked features of typical *P. virginica.* There is an almost constant association with *Anomodon,* although the species occasionally occurs on damper, noncalcareous ledges, associated with *Metzgeria hamata* and *Lejeunea laetevirens* (*Schuster* 40567). When occurring under such mesic conditions, the separation from var. *caroliniana* becomes critical.

The type material of the species appears to be a very atypical phase (mod. *parvifolia-viridis-leptoderma*) only 1-2 mm wide (Evans, 1892), in which the dentition of the leaves is hardly normally developed, and in which the broadly ovate leaf shape is not fully realized (Fig. 43:1-4); there are fewer teeth than normal ("varying in number from 2 to 3 on each leaf, usually 4 or 5"); the aerial shoots are normally simple. The plants are also abnormal in lacking propagula, which typically are abundantly produced.

By contrast, the ramified, robust plants from South Carolina (*Schuster* 37625) are up to 4-5 mm wide, and apparently represent the mature state of the species. These plants occurred in abundance on the vertical faces of dry but deeply shaded, large boulders and ledges, which were at least weakly calcareous, associated with *Porella platyphylloidea, Porella pinnata* subsp. (an undescribed subspecies!), *Cololejeunea ornata, C. biddlecomiae, Radula andicola, R. obconica, Lejeunea laetevirens* and *Metzgeria conjugata* and *myriopoda.* The plants had smaller, blunter and shorter teeth of the leaves, but these were usually more freely developed, usually 4-7 per leaf, but in some cases the leaves were subentire except for two weak teeth at the subtruncate apex.

Differentiation.—The primary characteristics of this species are (a) the contiguous to moderately imbricate, usually ovate leaves, which (b) freely produce propagula on the postical, but never on the antical faces; (c) the leaves short-decurrent postically, leaving the stem typically extensively exposed; (d) the very small to ephemeral underleaves; (e) the widely spreading leaves; (f) the sparing branching, but with the ultimate branches of at least mature plants furcate and terminal in origin. The species is variable and the weak phases of extremely shaded conditions (mod. *parvifolia*) are particularly difficult to comprehend. No regional species of *Plagiochila* has been more misunderstood. Indeed, the many collections seen had all been assigned to other species (*P. sullivantii, P. ludoviciana*) and the only collection,

other than the type, which has been assigned to the species (Evans, 1896) represents still another species, *P. yokogurensis.*

In spite of having been widely confused with *P. ludoviciana* and *P. sullivantii, P. virginica* bears only the most general and superficial relationships to these species.

Fig. 45.—*Plagiochila virginica* Evs., robust phase with aerial branching, transitional to *P. v. caroliniana.* 1. Leaf (x 12); 2. Leaf, postical aspect, with propagula (x 12); 3. Median cells with oil-bodies (x 516); 4. Apex of mature shoot (x 15); 5. Shoot-sector, postical view (x 16.5); 6. Leaf (x 12); 7. Leaf, with propagula, postical aspect (x 17); 8. Cells near leaf-apex (x 212). (Figs. 2-4, 7-8 drawn from plants from Whitewater R., S. C., *Schuster* 25108; figs. 1, 5-6 from *Anderson* 10338, N.C.; bracts and perianth of this type illustrated in Fig. 46:9-11.)

Although the plant agrees with *P. sullivantii* in the approximate angle (55-76°) at which the horizontal leaves spread from the stem-apex, as well as in the approximate cell-size and cell-type, and in the few but often sharp marginal teeth of the leaves, there are numerous characteristics separating the two. Therefore, the statement by Frye and Clark (*loc cit.*, p. 440), in which doubt is expressed as to the distinctness of *P. sullivantii* from *P. virginica* can only be interpreted as indicating a lack of comprehension of these taxa. *P. virginica* differs from *sullivantii* not only in the constantly green color and the dull texture, but in the mode of asexual reproduction (*via* propagula of the persistent leaves), in the relatively numerous oil-bodies per median cell, and in the basic leaf-shape (ovate to ovate-rectangular, vs. obovate). Any close relationship between the two is quite unthinkable.

Although the species bears certain similarities to *P. ludoviciana* (basic leaf-shape, dentition, leaf-proportions, mode of asexual propagation, etc.), it differs from this species in several significant features: in the much less closely imbricate leaves (with the stem, in postical aspect, widely exposed); in the short-decurrent postical leaf-bases, which are not at all squarrose or reflexed; in the smaller size of the plant; and in the minute underleaves. Only rarely are obvious, laciniform underleaves present.

P. virginica also bears certain superficial similarities to, but is not closely related with *P. columbiana*. It was keyed out with this in Evans (1896). The much smaller leaf-cells at once separate *P. virginica* from *P. columbiana* (which agrees with *P. arctica* in having the largest cells of all our species, averaging *ca.* 38-42 μ in the leaf-middle, occasionally more). *P. virginica* also differs from *P. columbiana* in having more distinctly ovate, more elongate leaves (at least 1.2-1.5 $\times$ as long as wide, even on juvenile leaves), and apparently in never showing well-developed underleaves.

Most underleaves are very small in *P. columbiana,* but as Evans points out, a few are large and lanceolate. Such underleaves are quite unknown in *P. virginica.* Frye and Clark attempted to separate *P. virginica* on the basis of "underleaves wanting," which Evans also indicated to be the case in his original diagnosis. However, an isotype of *P. virginica* shows occasional underleaves, consisting of 1-2 uniseriate filaments 2-4 cells long, each tipped with a hyaline slime-papilla; much of the other material seen had obvious underleaves. No separation appears possible on that basis. Furthermore, the Unicoi Gap material is clearly provided with underleaves. The most important character differentiating *P. virginica* is the ability of the species to produce propagula (which *P. columbiana* is quite unable to form). Any close relationship between these two species is improbable.

The poorly developed type material also shows relatively slight dilation of the postical leaf-bases, with portions of the postical margin, in extreme cases, nearly parallel to the antical margin. Such plants, furthermore, often have only 1-2 teeth on the postical margin, while the apex is sharply bidentate or almost bilobed (Fig. 43:1-4); such plants could give rise to confusion with *P. austini,* and might be regarded as a deviant, atypical form of the latter. However, the broader leaf-form, the total lack of caducous leaves, the green color, and the abundant reproduction by leafy propagula, as well as the ovate

leaf-form of well-developed plants and the dull texture prohibit confusion.

In addition to confusion in the literature (and in herbaria) with the preceding species, the writer has also seen material of *P. yokogurensis* subsp. *fragilifolia* misdetermined as *P. virginica*. However, *P. virginica* differs in several important respects from *P. yokogurensis,* among them: the dull texture when dry; the antically shorter decurrent leaves, which are never conspicuously falcate; the persistent distal portions of the leaves. Dry plants are separable at a glance because of the very different texture.

Although there has been confusion in the American literature bebetween *P. virginica* and the preceding four species (*P. sullivantii, P. ludoviciana, P. austini, P. yokogurensis*), there is no immediate relationship with them. The species has been so consistently misunderstood in the American literature that no one has been able to obtain any accurate idea of what the name *P. virginica* actually meant. Indeed, its author shortly after proposing it confused the plant with the unrelated *P. yokogurensis!* Most of this difficulty originated in the fact that the type plants of *P. virginica* are so impoverished and ill-developed that only prolonged study of a long suite of specimens made it possible to demonstrate that the type plants were conspecific with the much more robust material here referred to it. As soon as this conspecificity was established, it became clear that the affinity of *P. virginica* was directly with the Mexican (and supposedly also West Indian) *P. contigua* Gottsche (1863, p. 30, pl. 14). Indeed, the writer is not yet convinced that *P. virginica* can be maintained as a distinct species, but may represent a mere Appalachian race of *P. contigua.* Until fresh material of the latter, from Mexico, becomes available, the two are maintained as distinct.

The two taxa agree in the virtual lack of underleaves (Gottsche fails to show them in his carefully executed figures; Evans specifically states "amphigastria none"), although it must be assumed that the obsolescent underleaves were overlooked by both workers. They also agree in the angle of orientation of the leaves; the leaf shape; their weakly imbricate orientation; the dentition of the leaves, and particularly the tendency for the leaves to be subtruncate at the apex; in the juvenile perianth with a weak and low antical wing of the basal half of the keel; the irregularly ciliate-dentate perianth mouth, and the shape of the bracts. Only three slight differences suggest that two distinct taxa are at hand: (a) the bracts in *P. contigua* are more fully and regularly serrate-dentate, with the teeth *ca.* 20-26 teeth per bract; (b) the perianth-mouth, judging from Gottsche's drawing, bears narrower and more acuminate teeth; (c) the vegetative leaves tend to have the postical margin more freely dentate, often with 2-8 teeth. In *P. virginica,* well-developed plants often have only 2-5 teeth of the whole leaf, of which only 1-2 occur on the distal half of the postical margin. However, this is not always the case (Figs. 46:4, 45: 1-2, 4). In view of the demonstrated great variation in *degree* of dentition of perianth-mouth, leaves and bracts in *P. ludoviciana* the claims of *P. virginica* for recognition as a species remain very weak indeed.

In addition to the very close affinity to *P. contigua, P. virginica* also appears directly related to another Mexican species, *P. xalapensis* Gottsche, a species with more decurrent antical leaf bases, and sharper, stronger dentition. More distantly allied are *P. subconvoluta* Gottsche, a species with almost perfectly oblong ♀ bracts and a more finely ciliate-dentate perianth-mouth, and probably also *P. muelleriana* Gottsche, also a species with a more closely, finely and freely ciliate perianth-mouth.

Variation.—Since this species was described from a leptodermous completely atypical extreme, the range of variation of the species is difficult to comprehend. The writer, at first, was of the opinion that *P. virginica* could represent juvenile material of several species, and therefore should be dropped as a *nomen dubium*, but now believes that the Unicoi Gap plants, those from South Carolina, and those from Linville Caverns, North Carolina, treated below, may well represent the typical form of this species. Collections in West Virginia, from near the type station, are needed to confirm this hypothesis. The Ammons work on West Virginia hepaticae (in which *P. virginica* is mentioned only among the excluded species) does not help at all in indicating the identity of *P. virginica*. The writer therefore suggests that, for the present, the materials collected by the writer in South Carolina, at Linville Caverns, North Carolina, and at Unicoi Gap, Georgia, and the plants collected in Giles County, Virginia, by the writer and by Patterson, be considered as "typical" of the species.

The species varies from a leptodermous extreme (type material; probably from an unusually moist site) to moderately pachydermous, with relatively small or moderate trigones, that may be moderately bulging (North Carolina, South Carolina, and Georgia plants). The most pachydermous type seen, represented by plants from Virginia (near Hot Springs, on limestone near stream, The Cascades, Bath Co.; *Patterson* 1448) has the trigones rather obviously bulging in most cases, with the longitudinal walls of median and basal cells sometimes evenly thick-walled. These plants are unusually robust (up to 4 mm wide), show an occasional dichotomization of the leafy aerial shoot system, and possess no propagula; they form a close approach to *P. virginica* var. *caroliniana*, but are still clearly *P. virginica*. Identical with these plants are those from South Carolina (Fig. 45, 46:9-11). The ability to develop trigones appears to require a relatively intense stimulus, in this taxon (compared to the related *P. virginica* var. *caroliniana*). In the Linville Caverns plants (*Schuster* 29043), for instance, the trigones are concave-sided and small: yet the plants grew under xeric conditions, near the crest of a cliff, in partial sun, associated with such xerophytic Hepaticae as *Radula complanata* and *Frullania squarrosa* (as well as xerophytic ferns, *Asplenium resiliens* and *Polypodium polypodioides* var. *michauxiana*). In the Georgia plants, from even more xeric sites (see section on Ecology), the trigones were barely bulging. One of the peculiarities of the typical species, therefore, is the inability to develop coarse, confluent trigones; the species thus exists chiefly as the mod. *leptoderma* and *mesoderma*.

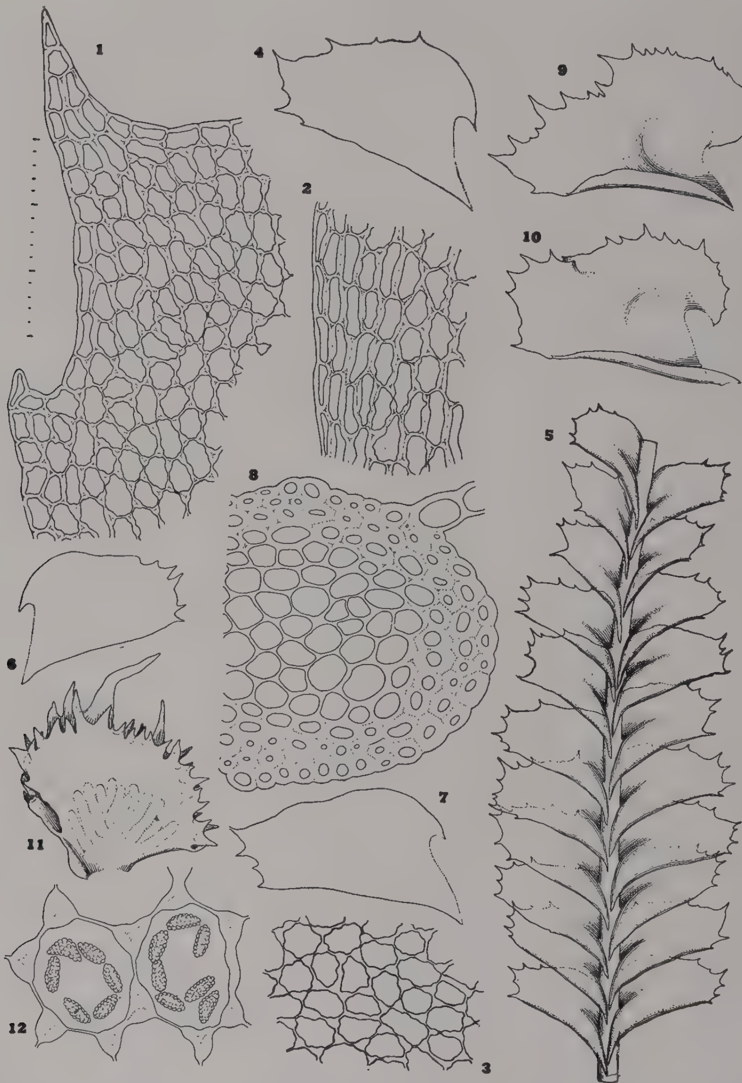

Fig. 46.—*Plagiochila virginica* var. *caroliniana* Schuster and transitional material to typical *virginica* (figs. 9-11). 1. Cells of leaf-apex (x 165); 2. Cells near postical base of leaf (x 165); 3. Median cells (x 165); 4, 6-7. Typical leaves (x 16); 5. Shoot (x 9); 8. Cross-section of stem (x 220); 9-11. Bracts and juvenile perianth, from one gynoecium, of form transitional to typical *virginica* (9-10, x 16; 11, x 33); 12. Median cells with oil-bodies (x 590). (Figs. 1-8 from *Anderson* 10338, Cullasaja Falls, N.C.; 9-11, from *Schuster* 25108, Whitewater R., S.C. [see also in Fig. 45]; 12, from *Schuster and Sharp* 34620, Blount Co., Tennessee.)

It is also evident, from the rather limited collections, that the plants are nearly always green, only the stems becoming brownish; the plants thus almost constantly are a mod. *viridis*. In general the dentition is not exceedingly coarse. The species appears unable to produce a narrow-leaved extreme, or mod. *angustifolia*. All plants seen were slightly imbricate-leaved or approximate-leaved, and had rather broad leaves. The range of modification, in this regard, therefore, is less than in var. *caroliniana*.

Perhaps the greatest degree of variation in this species occurs in the extent to which propagula are formed. In the type (probably from a mesic environment) no propagula are developed; in the xeric phase (Linville Caverns) we find that there is luxurious and abundant development of filiform propagula. As in *P. ludoviciana*, propagula production appears to be stimulated by increased difficulty in water uptake, and by more xeric conditions in general. This, present observations indicate, is the reverse of the situation in *P. virginica* var. *caroliniana*, in which propagula are frequent in the large phase from damp, shaded rocks (mod. *latifolia-viridis-mesoderma*), while the typical xeric extremes (mod. *augustifolia-colorata-pachyderma*) are almost or quite devoid of propagula.

The best developed material of the species which I have seen are the 4-5 mm wide plants from the Estatoe R. Ravine in South Carolina (*Schuster* 36625) and from the Whitewater R. Gorge in South Carolina (*Schuster* 25108). In both of these collections there are numerous gynoecia. Furthermore, they show an identical branching system as in *P. dubia:* the aerial shoots are produced as intercalary lateral branches from a creeping, more or less small-leaved rhizomatous system. Each aerial shoot may develop 1 or 2 monopodial, widely spreading, lateral intercalary branches, but eventually forks pseudodichotomously, the forks commonly becoming unequal in length, with at least one again forking, the branches being uniformly terminal. The ultimate branches, which are thus pseudodichotomously oriented, may be short (2-3 leaf-pairs) or elongated (6-12 leaf-pairs) before producing gynoecia. The gynoecia invariably produce a single subfloral innovation, which may remain sterile or may soon end in another gynoecium. In no case could gynoecia without subfloral innovations be found, or gynoecia with paired innovations (differing thus from *P. dubia*). Branching of the aerial shoot system is rare and sporadic, however, except in such robust female plants.

The copiously developed plants from South Carolina (referred to above) show a close and unmistakable similarity to *P. contigua* G. They agree in basic size, the form, dentition, and orientation of the leaves, and in the form of the immature perianth.

The preceding, leptodermous to mesodermous plants are very largely restricted to calcareous sites. Away from calcareous sites typical *P. virginica* is often supplanted by an xeromorphic type:

Plagiochila virginica var. **caroliniana** var. n.

Figs. 46:1-8, 12; 47

P. virginicae typicae similis; differt: planta minima, pauciramosus, olivacea, sicca plus minus brunnea; foliis angustius ovatis vel ovatis-rectangulatis; cellulae basales parietibus ± aequaliter incrassatis; cellulae apicales vel mediae ca. (16-

19) 18-21 (24) μ x 18-24 (26-30) μ, trigonis maximis, nodulosis. Typus: Bearwallow Creek, Toxaway Gorge, SW. of Rosman, North Carolina (*Anderson* 12823).

Plants green, with stems rigid and brownish, or the entire plant brownish (the *cell-walls of the leaves becoming quite yellowish*). Shoots usually $\pm$ dichotomously branched, (1.8) 2.5-3.5 mm wide usually. Stems rigid, *ca.* (130-180) 200-235 μ wide, with cortex strongly pachydermous, well-defined; dorsal and ventral cortical cells similar, bast-like, thick-walled, 10-12.5 μ in diameter x 42-75 (85) μ long; cortical cells in (2) 3-4 layers, rigid; medulla in 5-8 layers, the cells (14) 16-20 (24) μ in diameter, slightly collenchymatous; stem as a whole 12-16 cells high. Leaves distant to weakly imbricate, varying

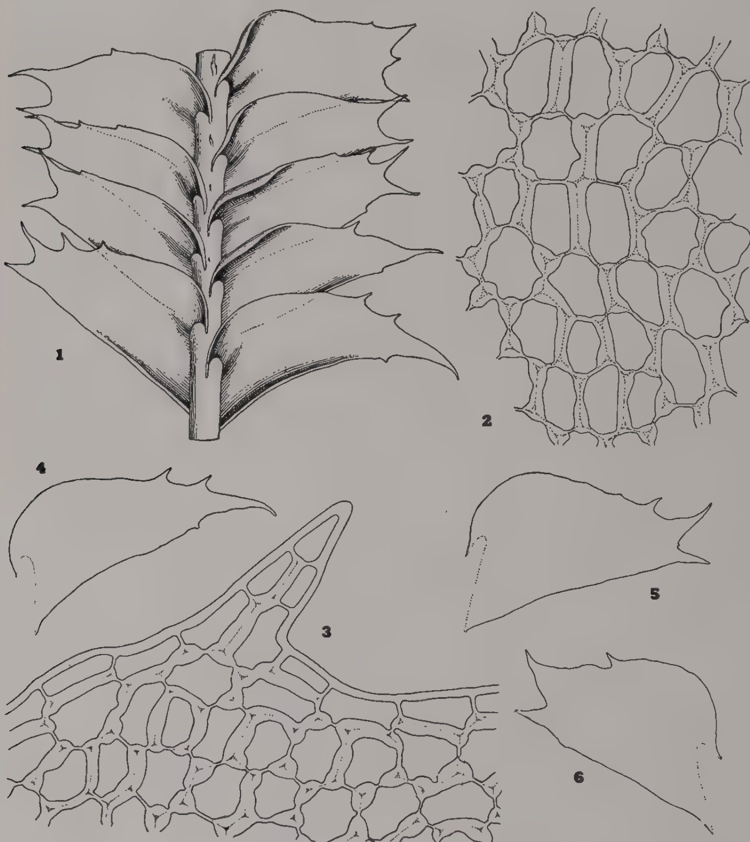

Fig. 47.—*Plagiochila virginica* var. *caroliniana* Schuster. 1. Shoot-sector, postical view (x 31); 2. Median leaf cells (x 400); 3. Cells of postical leaf-margin, above middle (x 400); 4-6 Leaves (x 31). (All from xeric, brown mod. *colorata-pachyderma-angustifolia*, from *Anderson* 8660.)

from rather broadly ovate (identical with those of typical *virginica;* up to 1350 μ wide x 1800 μ long) to *narrowly ovate-falcate* (then only 400-500 (650) μ wide x 800-1000 μ long, *averaging up to twice as long as wide*). Cells *strongly collenchymatous,* often with yellowish walls; cells along leaf-margins, *even near leaf apex, tending to be strongly* elongated in 1-2 rows; subapical and median cells tending to be smaller than in typical *P. virginica, ca.* (16-19) 18-21(24) μ wide x 18-24(26-30) μ long; cells along postical margin near middle of leaf *ca.* 13-16 (21) μ wide x 23-28 (36) μ long, those within margin nearly isodiametric and 17-21 (24) x 18-22 (25) μ long; cells at postical base becoming narrower and more prominently elongated; cell-walls of marginal 1-3 cell-rows *tending to become strongly and equally thick-walled,* near the postical leaf-base the marginal 3-6 cell rows similarly, strongly longitudinally thick-walled, the *cell lumens becoming nearly linear;* subapical, median and basal interior cells with coarse trigones, *those of leaf-middle and base tending to have the trigones strongly longitudinally confluent.* Oil-bodies mostly (2-3) 4-8 per cell and 4 x 6.5-8 μ, a few to 5 x 12 μ; in some cells 10-11 oil-bodies which are only 3-4 μ and spherical 3.5-4 x 5-6.5 μ; oil-bodies papillose-segmented; chloroplasts *ca.* 4 μ. Underleaves vestigial.

Female plants (2) 3-4 times dichotomously furcate, the gynoecia terminal on the ultimate branches, usually with innovations. Bracts similar to leaves, suberect to erect, the apices spreading, postical margin undulate, ovate-oblong, ampliate, *ca.* 1400-1500 μ long x 1150-1225 μ wide (the width difficult to accurately determine, due to the strongly postically involute antical margin); postical margin and apex very irregularly and coarsely dentate with broad-based, scarcely acute or subacute teeth (*ca.* 16-20 teeth per bract); the antical margin of bract entire. Juvenile perianth (*ca.* 900 μ wide at mouth) with short antical keel, unwinged, except above base and shorter, unwinged postical keel; transverse and truncate-rounded mouth closely and irregularly dentate with subacute to blunt, to angulate, broad-based teeth (teeth commonly 4-6 cells wide at base x 6-8 cells long), and with a few longer laciniae (10-12 cells wide at base x 20-30 cells long); cells of teeth essentially isodiametric.

Type.—Moist rocks, edge of stream, in shade, Bearwallow Creek, Toxaway Gorge, SW. of Rosman, North Carolina, 1100 ft. (*Anderson* 12823); in herb. Duke University; schizotype in author's herbarium.

Distribution.—*P. virginica caroliniana* appears to have a highly restricted distribution, at median elevations in the Southern Appalachians, at from 1050 ft. to *ca.* 3200 ft.

VIRGINIA: Sink Hole near Lucas Memorial Church, near Pembroke, Giles Co. (*Patterson,* July 1943!; listed by Patterson as *P. ludoviciana;* plants with relatively small trigones, grading into *P. virginica,* typical); near Big Cascades, on side of siliceous boulder, 3000 ft., Mountain Lake, Giles Co. (*Sharp V*-47; listed by Sharp, 1944, as *P. ludoviciana*). TENNESSEE: Lower Roaring Fork, above Gatlinburg, Sevier Co., 1700 ft. (*Sharp* 35265!, 1935; listed as *P. ludoviciana* in Sharp, 1939); Greenbrier Cove, at Porters Creek, *ca.* 2500 ft.,

Sevier Co. (*Patterson, July, 1947,* as *P. ludoviciana;* with *P. austini!*); above the Orchard, Mt. LeConte, Sevier Co., 2800 ft. (*Sharp* 3577); siliceous Boulder, Meigs Creek, Sevier Co., 2000 ft. (*Sharp* 36219); Greenbrier Pinnacle trail, Sevier Co., 2800 ft. (*Sharp* 341093) (the preceding Sharp collections all cited in Sharp (1939) as *P. ludoviciana*); shaded moist holes in bluff, along Little R. above Forks, towards Elkmont, Sevier Co., 1800 ft. (*Sharp* 515!); below Tremont, *ca.* 1600 ft., Blount Co. (*Schuster* and *Sharp* 34620). NORTH CAROLINA: Upper Falls, Whitewater R., Jackson Co. (*Anderson* 8660!; *Schuster* 25052; *p.p.,* with *P. sharpii sharpii*); below Cullasaja Falls, 9 mi. N. of Highlands, Macon Co. (*Anderson* 10388!); Bearwallow Falls, Toxaway Gorge, Transylvania Co. (*Anderson* 6660!); Crow Creek, Little Fishhawk Mt., NW. of Highlands, Macon Co. 3700 ft. (*Anderson* 7940! *c. per. juv.*); W. side of Whitewater R. gorge *ca.* 1/6 mi. below High Falls, Jackson Co. (*Schuster* 34731, 34737, 34736); underside of deep recess at one side of High Falls of Whitewater R., *ca.* 2800 ft., Jackson Co. (*Schuster, L. E. Anderson, W. D. Billings* 34730) (Cotype); below High Falls, Whitewater Gorge, Jackson Co. (*Schuster* 40568, 25052); east of Rich Mountain, on Mull Creek just above juncture with Beachflat Creek, *ca.* 2500 ft., Jackson Co. (*Schuster* 39684 *p.p.,* with *Radula obconica*); Cullasaja Gorge, NW. of Highlands, Macon Co. (*Sharp* 141!; in herb. Y as *P. ludoviciana;* a somewhat brownish phase, very typical, with narrow leaves; admixed with *Radula andicola*); rocks of stream, side of Grandfather Mt., below Yonahlossa Road (*Andrews* 53!; in herb. Y as *P. ludoviciana*). Possibly referable to var. *caroliniana* are the robust fertile plants from SOUTH CAROLINA: *Ca.* 0.5 mi. below Lower Falls, Whitewater R., north of Jocassee, Oconee Co. (*Schuster* 25108; *c. per. juv.!;* transitional to typical *P. virginica*).

Ecology.—A taxon restricted evidently to damp, shaded, humid gorges and the rocky banks of shaded streams; usually restricted to acidic rocks (unlike typical *P. virginica*). The mesic habitat is characteristic. In several stations occurring with *Mnium carolinianum, Jubula pennsylvanica, Metzgeria conjugata,* and (nearby) *Dumortiera nepalensis* and *hirsuta,* and the filmy fern, *Trichomanis petersii.* Elsewhere found admixed, or in juxtaposition to *Plagiochila yokogurensis fragilifolia* and *P. austini;* occasionally on damp, shaded rocks associated with *Radula obconica* and *Fissidens* sp.

The strongly xeromorphic structure, with bast-like cortical stem cells, and strongly collenchymatous leaf-cells, *in spite of the restriction to damp sites,* is remarkable. As we have seen under *P. virginica,* typical, the latter often is found on dry calcareous rocks, often relatively exposed, yet has a green color throughout, little-thickened cortical cells, and little-collenchymatous leaf cells. This suggests that two physiologically different taxa are at hand. Unfortunately, the different behavior patterns are not absolutely correlated with sharp morphological distinctions.

Variation.—This taxon appears to show considerable variation in robustness and color, correlated with the isolation and saturation-deficit of its habitat. Three types of plants are distinguishable, on the basis of the available material.

(1) Mod. *viridis-latifolia-megafolia-mesoderma vel pachyderma.*—In this form, the entire plant is greenish, although the stems may be brownish-green; the shoot is wide, (1) 2-4 × dichotomous, the leaves relatively imbricate and

strongly antically decurrent (and the plants thus acquire the facies of *P. ludoviciana*). The cell-walls of this phase bear distinct and bulging trigones, which are, however, relatively small and sharply defined, never becoming confluent; plants of this type freely bear propagula. This material is represented by the South Carolina specimens as well as by several others (Upper Falls, Whitewater R., Jackson Co., North Carolina, *Anderson* 8747, DU; east of Rich Mt., on Mull Creek, Jackson Co., *Schuster* 39684). The most luxuriant development of these plants shows free furcate branching. These plants are transitional to "normal" *P. virginica* (Figs. 45, 46:9-11), and should perhaps be referred to it.

(2) Mod. *colorata-angustifolia-pachyderma-propagulifera.*—This type is represented by brownish plants (leaves brownish-green, but stems reddish-brown), with coarse confluent trigones, somewhat yellowish in color; the leaves are at times narrower than usual, often merely approximate; the shoots are smaller, usually 2.5-3 mm wide. Plants of this type bear propagula very intermittently. This material is represented by specimens from North Carolina (below High Falls of Whitewater R., Jackson Co., *Schuster* 40568; and below Cullasaja Falls, 9 mi. N. of Highlands, Macon Co., *Anderson* 10338; DU). (Fig. 46:1-8, 12.)

(3) Mod. *colorata-parvifolia-angustifolia-pachyderma-epropagulifera.*—This represents the extreme xeric phase of the species (plants strongly brownish, particularly the stems; leaves small, and plant poorly developed, only 1.8-2 mm wide; propagula not at all produced; cells with trigones confluent, the more elongate cells usually with the trigones confluent on the longitudinal walls to a point where the *bursata*-type of cell is simulated). These plants bear no resemblance at all to *P. ludoviciana* or *virginica,* but are apt (because of size, distant and narrow leaves, somewhat shining brownish color) to be mistaken for *P. austini.* This third type of plant is represented by two collections from North Carolina (Bearwallow Falls, Toxaway Gorge, Transylvania Co., *Anderson* 6660; Duke; and Upper Falls, Whitewater R., Jackson Co., *Anderson* 8660). (Fig. 47.)

The plants of the extreme xeric type would scarcely be considered related to the mesic extreme (type 1), were it not for the presence of intermediate plants (type 2), which clearly bridge the gap. The recognition of this taxon is most easily achieved when plants of types 2 or 3 (*i.e.,* the more xeromorphic forms) are at hand. These plants, in their strong pigmentation, and excessively strongly collenchymatous cells, differ from all our other species (except the pachydermous extremes of *P. sharpii*). In none of our other species are the trigones so salient, so freely confluent, and in no other case is the extreme *bursata*-type of cell simulated. However, the marginal cells of several species show a tendency for the development of equally thickened longitudinal walls (*e.g.,* in *P. diffusa*). Confusion with these species is scarcely possible, because these species have strong thickening of the cell-walls confined to the marginal cells.

The plants of type 3 are also characterized by the partly extremely narrow leaves (*ca.* 400-500 μ wide x 800-1000 μ long; averaging twice as long as wide, often acuminate distally or sharply bilobed. Such phases, furthermore, have the marginal cells usually strongly elongate and thick-walled, thus forming a border (and in this respect simulating *P. diffusa*). The narrow leaf-form, in such plants, is further correlated with a lesser development of the postical base, which is only slightly dilated. The width of such xeromorphic plants usually does not exceed 1.8-2.1 mm. The combination of brown color, narrow (and sometimes scarcely approximate) leaves, and the small size all suggest the quite unrelated *P. austini.*

P. virginica var. *caroliniana*, as here circumscribed, may prove to be a composite taxon. The aerial shoots of the fertile plants of type 1 are quite regularly 2-4 × pseudodichotomously (less often more nearly monopodially) furcate, and bear juvenile perianths. In them there is no marked tendency for the trigones, which are sharply defined, to become confluent, except at the postical base. These plants have exceedingly small cells of the leaves; averaging on fully mature, fertile shoots only 16-19 x 18-22 (24) μ in the leaf-middle. These plants appear closely allied to the mod. *mesoderma* of typical *P. virginica*.

All the other collections seen are of plants that are sterile with virtually unbranched or rarely monopodially branched aerial shoots. They tend to have larger leaf-cells, averaging from 19-23 μ wide medially, and the cell-walls of the leaves manifest a strong tendency to become longitudinally confluent. This tendency is most strongly evident in the marginal and submarginal cells, from the apex to the leaf-base. These cells then become equally thick-walled. No such tendency whatsoever occurs in the South Carolina material (Fig. 45:3, 8), which is transitional to "normal" *P. virginica*. The larger-celled plants, with often confluent trigones, grade somewhat into typical *P. virginica*. Possibly some of them may prove to belong to that species, as mere xeromorphic manifestations. The exceedingly mesic habitat, and strongly collenchymatous cells, of the type plants of *caroliniana* make it impossible to explain these as a mere environmental modification, however.

Clearly, the variability of the *P. virginica-caroliniana* complex remains a subject needing careful field study and fuller collections than now available.

In the last several years I have alternately considered var. *caroliniana* as a mere modification, or a full-fledged species. The collections made under the High Falls of the Whitewater R., North Carolina (*Schuster* 40567, 40568) suggest that two species may be at hand. On more exposed rocks occurs a green, mesodermous phase, without confluent trigones of the basal half of the leaf; these plants show regularly 1-2 dichotomous forks of the aerial stems, and tend to form patches. By contrast, on the underside and vertical faces of undercut, humid ledges occurs a much smaller plant, whose creeping primary stems produce at intervals erect (or pendent), unbranched, short leafy axes; the leaves are coarser-toothed and fewer-toothed; the stems are more rigid and brown; the basal halves of the leaves have very largely confluent trigones and more elongate-appearing cells. The latter plants, typical var. *caroliniana*, grew within 16-20 ft. of typical *P. virginica*!

The separation of plants of the "extreme" *caroliniana* type from small phases of *P. sharpii* is sometimes impossible in the field, the two being identical in facies. A small collection of *P. sharpii* from Cullasaja Falls (*Schuster* 49737) is a case in point. The plants agreed with *caroliniana* in being short (8-12 mm high usually), slender (1.5-2.1 mm wide), brownish-tinged, and in growing diffusely, the creeping stolons producing unbranched, erect, leafy axes at considerable intervals. Under the microscope the marginal cells were collenchymatous, exactly as are the inner cells, and the vitta was hardly distinct — as is often the case with very weak phases of *P. sharpii*. However, the smaller cell size (subapically 16-18 μ wide), the sharply nodulose trigones, and in particular the homogeneous oil-bodies served to place the plants into *P. sharpii*.

Plagiochila virginica var. **euryphylla** var. n.
Fig. 48

P. virginicae typicae similis, praesertim ad virgas tenuis vel juvenilis, sed differt aspectu magis pellucido; foliis latissime dilatatis, late ovatis vel ovato-triangularibus (0.9-1.33:1), ad virgas robustas dense imbricatis; foliorum marginibus subintegris vel obscure dentatis; folii basi ventrali valde undulata, P. undatae simili. Typus: Windy Falls, Horsepasture R., Transylvania Co., North Carolina (*Anderson* 8480).

Plants rather robust for *P. virginica,* up to 3-4 mm wide x 1.5-3 cm long, the aerial shoots nearly simple. Weak shoots somewhat similar to *P. virginica,* but the robust ones with much broader, more dilated, broadly ovate leaves that are somewhat wavy or crisped and have broadly deflexed postical leaf-bases. Stems *ca.* 300 μ in diameter, green to light brownish, without rhizoids except rarely below. Leaves varying from broadly asymmetrically ovate and 1300-1320 μ long (from insertion) x 1400-1520 μ broad to 1400-1500 μ broad x 1450-1575 μ long (*length, on the smaller, more broad-leaved shoots ca.* 0.9-1.1 $\times$ *the width*); the larger leaves to 1500 μ wide x 2000 μ long (*length* 1.33 $\times$ *the width*) and more narrowly ovate; postical margins strongly arched, quite dilated above base, nearly straight distally; antical margin usually nearly straight; both antical and postical margins more or less *strongly deflexed, especially the postical base which is erect or often broadly recurved* (*the leaf, as a consequence,* normally rather strongly convex dorsally and *hollowed in postical aspect*); outer portions of postical margin often somewhat undulate or crisped; *leaf-margins subentire to paucidentate, the often broadly truncate apex* with at best a few obscure, low, often rounded teeth, under maximal conditions with 3-5 rather obscure apical and subapical teeth; *leaves strongly imbricate,* on older and more robust portions of shoots the dilated and shingled *leaf-bases often virtually or quite hiding stem.* Cells distinctly collenchymatous, the subapical *ca.* 21-24 μ, the median *ca.* 21-24 (25) x 24-28 (32-34) μ; *those of the very short-decurrent postical base hardly differentiated,* mostly only 1.3-1.8 $\times$ as long as broad, *ca.* 18-20 μ wide x 22-30 μ long, rather thick-walled, at least as regards longitudinal walls. Underleaves minute, of a few cilia tipped with hyaline papillae, disappearing with age. Asexual reproduction via propagula present, but rare and local.

Type.—Moist rock, below Windy Falls, Horsepasture River, near Cashiers, Transylvania Co., North Carolina, *ca.* 2000 ft. (*L. E. Anderson* 8480; Aug. 20, 1949). In herb. Duke; schizotype in herb. author.

Distribution.—Known only from the type collection. Probably endemic to the restricted escarpment region of the Southern Appalachians, and restricted to the Mixed Mesophytic Cove Forest Region, to which *Mnium carolinianum* is also endemic.

Differentiation.—A distinctive taxon, characterized by the dense, strongly ampliate, broadly ovate, paucidentate leaves, which are long-decurrent antically, but short decurrent postically. The broadly ovate-triangular and subentire leaves suggest a similarity to *P. undata.* This

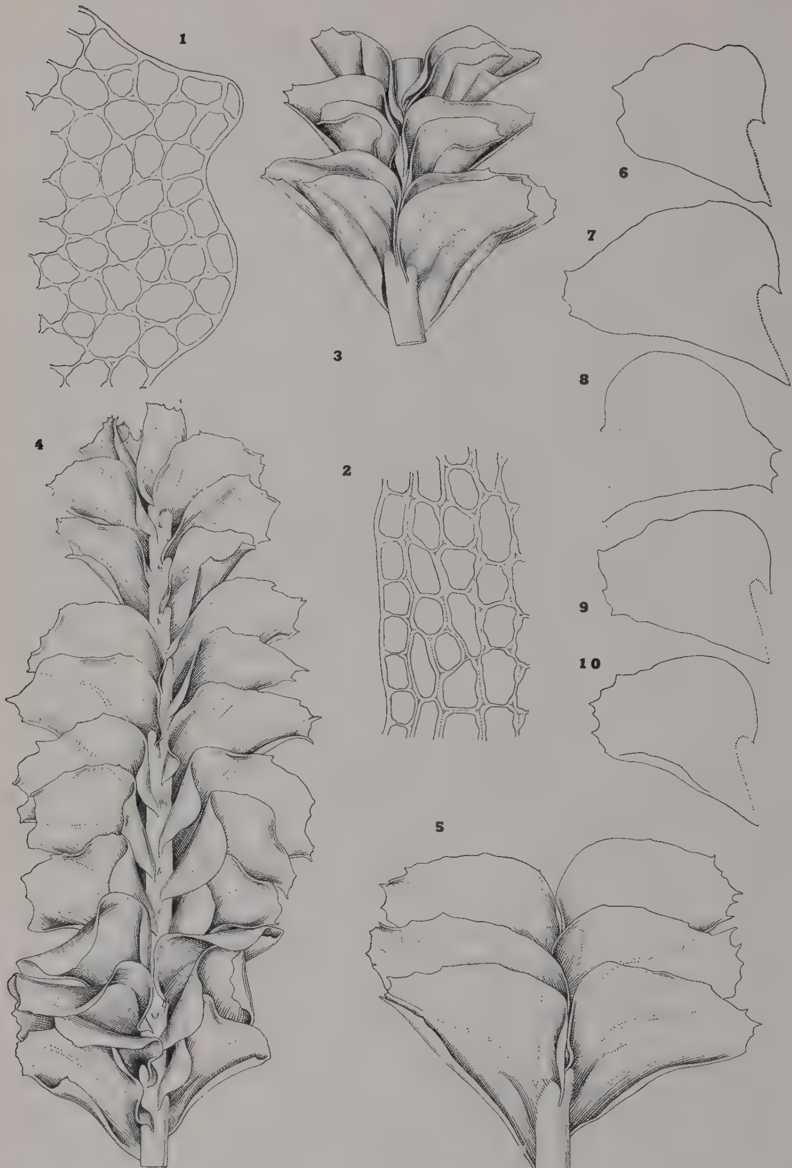

Fig. 48.—*Plagiochila virginica* var. *euryphylla* Schuster. 1. Cells of leaf-apex (x 232); 2. Cells of postical leaf-base (x 232); 3. Sector of dense-leaved extreme, postical aspect (x 12); 4. Typical shoot, postical aspect (x 12); 5. Robust shoot-sector, postical aspect, with approach to typical *P. virginica* (x 12); 6-10. Leaves (x 12.5; 6, 8-10 normal leaves of dense-leaved shoots; 7, leaf of robust extreme). (All drawn from type material, Horsepasture R., N.C., *Anderson*.)

similarity to *P. undata* is enhanced by the closely imbricate leaves, their strongly postically secund orientation when dry (an orientation which persists to some degree when the plants are moist, as a consequence of which they look strongly convex antically, strongly concave postically), and by the somewhat circinate coiling of the shoot-apex in drying. The postically secund leaves and the somewhat coiled or deflexed shoot-apices (when dry) also suggest *P. hypnoides,* a species which also agrees in the short decurrent, imbricate, postical leaf-bases.

These similarities to *P. undata* and *P. hypnoides,* however, are quite superficial. *P. virginica euryphylla* differs at once from *P. undata* in the short-decurrent postical leaf-bases, and in the minute underleaves, as well as in the much less markedly undulate postical leaf-margins. The broadly ovate leaf-shape, the reduction of the dentition, and the obsolete underleaves at once separate the species from *P. hypnoides.*

The relationships of *P. virginica euryphylla* are with the Contiguae, rather than with the Hypnoides and Crispatae. These relationships to the Contiguae are indicated by (a) vestigial underleaves; (b) cell size and bulging trigones; (c) rather weak dentition, absent near the postical leaf-bases; (d) ovate leaf form; (e) segmented oil-bodies; (f) very short-decurrent postical leaf-base; (g) presence of propagula on the postical leaf-faces.

Among the Contiguae, *P. virginica euryphylla* appears to be related most immediately to the *P. virginica-caroliniana* complex. The shorter and broader, postically more ampliate leaves, the denser insertion of the leaves, and particularly the similarity in facies of mature plants to *P. undata* separate *P. virginica euryphylla* from the immediate vicinity of other members of this complex. In none of the numerous collections of the *P. virginica-caroliniana* complex seen was there an equally marked tendency for the teeth of the leaves to become obsolete as in var. *euryphylla.* A more distant relationship may occur with the two Mexican species, *P. stolonifera* and *P. anomala* L. & G. *P. virginica euryphylla* has a leaf-shape which closely approaches that of these two species. As in *P. anomala,* some leaves are entire and obtusely pointed at the apex; as in *P. stolonifera,* other leaves bear a few teeth distally. In some respects, *P. virginica euryphylla* falls midway between these two Mexican species in respect to the leaf-shape. However, the leaf-cells of *P. anomala* are very different, according to Gottsche (1863), and the dentition of the leaves in *P. stolonifera* is more copious, extending to near the postical leaf-bases. The absence of comparative material of these two taxa makes a further comparison useless. It should be noted, however, that Stephani (1905, p. 596) transferred *P. anomala* to *Syzigiella.* Stephani also described the cells of *P. stolonifera* as very strongly collenchymatous, eliminating that species from further consideration.

The mature shoots of this taxon are so very different in facies from any form of *P. virginica* which I have seen that originally the plants of the present variety were considered to be a distinct species. However, less well-developed plants show a strong similarity to *P. virginica*

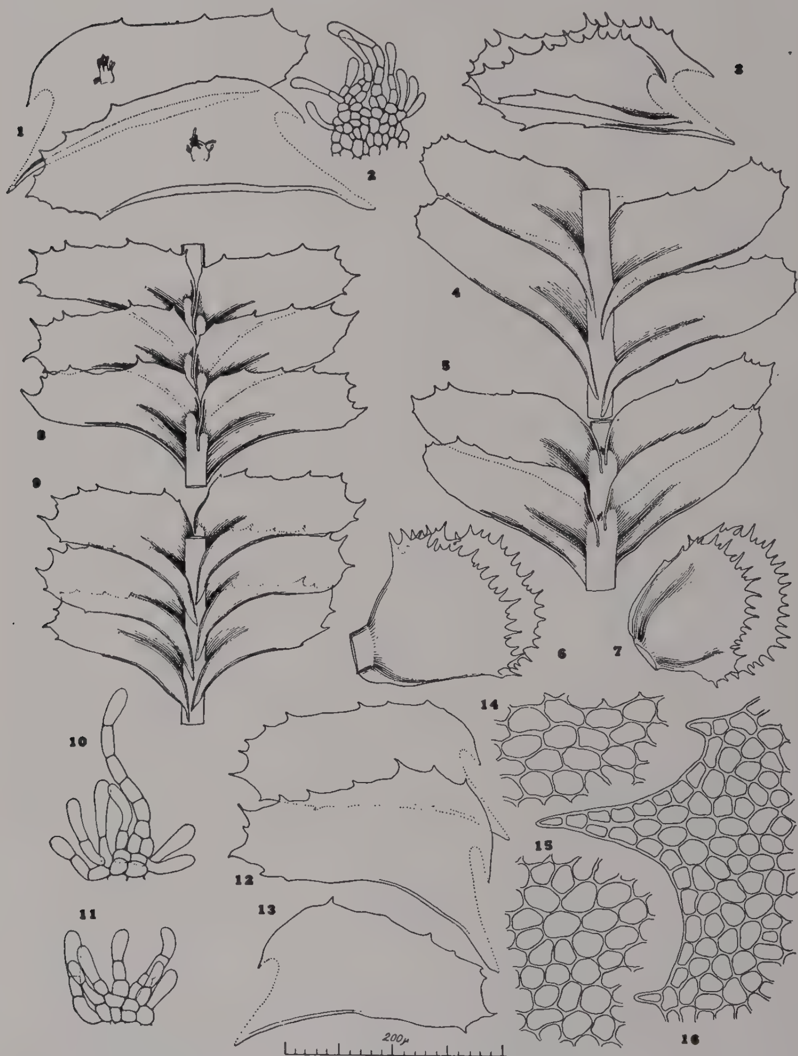

Fig. 49.—*Plagiochila dubia* Gottsche. 1. Two leaves, with maximal sized underleaves drawn to same scale (x 18); 2. Large underleaf (x 78); 3. Female bracts, immature in size (x 18); 4. Shoot-sector of robust plant, antical aspect (x 12.5); 5. Same, postical aspect (x 12.5); 6-7. Juvenile perianths in lateral view (x 18); 8-9. Shoot-sectors of coarsely dentate phase, postical and antical aspects (x 12.5); 10-11. Normal underleaves (x 142); 12-13. Leaves (x 18); 14. Cells below leaf-apex (x 142); 15. Cells near leaf-middle (x 142); 16. Cells of leaf-apex (x 142). (Figs. 1, 3, 6-7, 12-13 drawn to one scale; figs. 4-5, 8-9 drawn to one scale; figs. 10-11, 14-16 drawn to scale at bottom of plate; figs. 1-7 from *Schuster* 33475a, Devil's Millhopper, Florida; 8-16, *Schuster* 33537, Alum Bluff, Florida.)

var. *caroliniana*. Until more copious collections of var. *euryphylla* are found, it seems best to give it only varietal rank.

As is noted elsewhere, *P. virginica* as delimited here is now an extremely polymorphous taxon and may well prove to embrace two or more species when the variability of its members is studied experimentally. It is possible that the unique development of the present plants is in part influenced by anomalous environmental conditions. Whatever the future status of the plants, the included plate clearly shows the differences they exhibit, as contrasted with *P. v. virginica* and *P. virginica caroliniana.*

PLAGIOCHILA DUBIA Lindenb. et Gottsche
Figs. 49-52; 53:6-8

Plagiochila dubia Lindenb. et Gottsche, *in* G. L. et N., Syn. Hep., 630, 1847; Gottsche, Mex. Leverm. 16, Pl. II, figs. 1-8, 1863.
Plagiochila floridana and *P. austini,* in part, of certain American authors.

Plants pure to somewhat olive-green, the stems ± olive-brown to brown, *dull,* typically forming loosely prostrate patches, on trees or on rocks, the leafy shoots ascending or arching away from substrate, simple or *loosely pseudodichotomously furcate;* branches widely spreading; gynoecia usually with 2, less often with 1, subfloral innovations (which may again be swiftly floriferous, and again bear innovations, leading occasionally to the formation of dendroid branch-systems at the apices of female branches). Main shoots varying from 3.2-4.2 mm wide (on xeromorphic extremes, and in plants from the periphery of the range sometimes only 2.0-3.2 mm wide); stems slender, (190-200) 240-275 μ in diameter. Rhizoids very few. *Leaves when moist contiguous to slightly imbricate,* occasionally moderately imbricate, in drying deflexed, *somewhat convolute-twisted, and appearing quite remote,* quite linear, when moist *erect-spreading* (45-55°) *on the upper leaves,* in xeromorphic, small-leaved extremes also sometimes on the lower leaves, normally on mature stems with *lower leaves obliquely spreading* (65-75° usually), *but with postical margins almost invariably remaining at an acute angle* (65-80°, rarely 85°) *with* stem; leaves very *narrowly, obliquely ovate-lingulate,* on juvenile leaves and on weak stems sometimes more distinctly ovate, *widest clearly in the basal fourth, the postical margin weakly but distinctly ampliate above the base,* nearly straight above the dilation and *slightly and gradually converging to the nearly straight antical margin,* the leaves slightly and gradually, but *perceptibly narrowed from the basal fourth* to the rounded-truncate apex; leaves of mature shoots ranging from 775-850 (900-970) μ wide x 1600-1800 (2000) μ long, *averaging* (1.9) 2.0-2.25 (2.4) × *as long as broad,* on xeromorphic shoots sometimes only 740-850 x 1240-1360 μ long; *postical leaf-bases very short-decurrent,* the narrow decurrent strip and margin immediately above *narrowly erect, but not reflexed, the stem remaining prominently exposed;* dorsal base rather long-decurrent (weak forms) to prominently long-decurrent (strong forms), the antical margin narrowly but sharply reflexed for at least

half the length of the leaf; leaves normally *rather weakly serrate-dentate,* the dilated *postical base without teeth,* or rarely with a single obscure one, the postical margin above base usually with (3) 4-6 (7) low but sharp teeth, the narrowed apex usually with 2-4 teeth, of which 1-2 may be considerably larger, but hardly lobe-like, the distal one-fourth of antical margin commonly with (0) 1-2 weak teeth. Cells with walls ± thin, the trigones varying from moderate and concave-sided to rather large and bulging, not or exceptionally subconfluent, with intermediate thickenings absent except from leaf-middle, where rare, to base, where frequent; apical cells *ca.* 18-20 x 20-23 (25) μ; median cells (18) 21-24 x 24-32 (34) μ; cells at middle of postical margin 15-20 x 23-32 μ, their tangential inner walls not or hardly thickened; basal cells 22-24 x 29-38 μ or to 32-45 μ long; cells of teeth little elongated, the terminal acute triangular, *ca.* 21-24 μ long x 12-15 μ. *Oil-bodies very coarse-segmented* (more so than is normal for *P. floridana*), often only 2-4 or 3-5 segmented, the segments large and in a single row, occasionally with 6-9 segments, and then segments in part in two rows, 4-9 per cell, usually ovoid or ellipsoid to fusiform, 3 x 6-7.5 μ to 3-4 x 12.5 μ, rarely to 4.5 x 10 μ; chloroplasts 3-3.5 μ. *Underleaves superficially appearing nearly or quite absent,* obsolescent, in actuality reduced to 1-several minute cilia, of which one may be somewhat elaborated, ending in slime papillae, never with conspicuous lamellate lacinia. Asexual reproduction via *propagula,* produced from the distal portion of the postical faces of the leaves, and *often also on antical leaf face,* adjacent to postical margin.

Dioecious. Male plant unknown. Gynoecial plants with usually 2 subfloral innovations that may be again swiftly floriferous, and again bear innovations, leading to ± complex gynoecial systems. Bracts narrowly ovate-lingulate, similar in shape to leaves, (1450) 2150-2250 μ long x (780) 1000-1150 μ broad, often slightly falcate, *sharply but not coarsely spinose-dentate, the postical base often with rather crowded but smaller spinose teeth* (usually 4-6 per bract), but sometimes with only 1-2 teeth, the postical margin above base with 9-12 unequal, strong teeth; narrowed apex with 2-3 teeth usually; the antical margin revolute to or nearly to apex, with 2-5 small but sharp serrations. Perianth (unfertilized only seen) 1350 μ wide near the broadly rounded-truncate mouth x 1800 μ high, *irregularly but not very closely spinose-dentate, the teeth not crowded,* not laciniform, slender, ending in 4-6 superposed, single cells; dorsal and ventral keels subequal in length, the *antical obsoletely to distinctly winged for most or for its entire length,* the wing ending as a dilated auricle inserted on stem below, usually *with a few minute serrulations near apex.*

Type.—"Mexico apud Colipa" (*Liebmann*). The type material, in the Gottsche Herbarium at Berlin, has been destroyed. I have not seen duplicates of the type collection (or schizotypic plants); therefore, the diagnosis has been derived almost wholly from Floridian plants (*Schuster* 33324, Aspalaga Bluff, Gadsden Co.).

Distribution.—A neotropical species, restricted in the United States to a limited region of the outer Coastal Plain, extending from Louisiana to central and (somewhat questionably) southern Florida, northward represented by deviant but evidently conspecific material from South Carolina and North Carolina, where rare and local.

Apparently largely restricted to the West Indies and Central America, ranging from Mexico (*Liebmann, fide* Gottsche), to Puerto Rico (*Sintenis;* also a specimen seen from Laguna San José, Rio Piedros, *Pagan* 416), Cuba (*Wright*), southward to Valencia (Venezuela? *Fendler, fide* Stephani), and Bolivia (Tres Cruces, Cord. de Sta Cruz, 1400 m., *Herzog* 3556, *fide* Herzog and *fide Stephani!*). Typical, robust female plants have also been seen from Puerto Rico (Aibonito, *Pagan* 577!, mixed with *P. hypnoides*).

In the United States not previously reported. The following records of material that is presumably conspecific:

FLORIDA: "Buzzards Roost," W. of Gainesville, Alachua Co. (*Schuster* 33416, 33417, 33360); Aspalaga Bluff, on Apalachicola River, Gadsden Co. (*Schuster* 33324); "Devil's Millhopper," NW. of Gainesville, Alachua Co. (*Schuster* 33475, 33475a, 33476, 33480; *Anderson* 5271!); on *Hicoria,* Aucilla R. at Nuttall's Rise, Jefferson Co. (*Kurz* 128!; listed as *P. floridana* in Kurz & Little, 1933); Gainesville (*N. L. T. Nelson* 57, 57A; with perianths; listed as *P. floridana* in Kurz & Little, 1933); Highlands Hammock State Park, 6 mi. W. of Sebring, Highlands Co. (*Schuster* 19954b, *plate*!; 20106a, 26301, 26004, 26014, 26011a, *all var. integrifolia*); hammock forest at Juniper Springs, Ocala Ntl. Forest, Marion Co. (*Schuster* 31934); hammock forest near Hillsborough River, Hillsborough River State Park, Hillsborough Co. (*Schuster* 33937); Alum Bluff, Apalachicola River, Liberty Co. (*Schuster* 33537); deep hammock forest, Collier-Seminole State Park, Collier Co. (*Schuster* 26179a; var. *integrifolia*); Section 24, Long Key Pineland, Everglade Key, Everglades National Park, Dade Co. (*Schuster* 22050, 22097; var. *integrifolia*). LOUISIANA: Bois Lobbe (*Langlois* 622!; in herb. Yale as *P. smallii* Evs.; material sparse, but with both antical and postical propagula, with rather widely spreading leaves; trans. ad *P. floridana*?); near St. Martinsville (*Langlois* 622!; superficially trans. ad *P. floridana,* but leaves lingulate-ovate).

Less certainly to be referred here, but almost surely conspecific are plants from:

MISSISSIPPI: Over moist shaded, sandstone-limestone ledge, *ca.* 2 mi. E. of Route 49, near Saratoga, Simpson Co. (*Schuster* 19167a; questionable, see *P. floridana*). LOUISIANA: Base of gum tree, Sulphur Springs, near Covington, St. Tammany Parish (*F. Pennebaker,* B-3!). SOUTH CAROLINA: Swamp 8 mi. S. of Bamberg Co. (*Schuster* 33982, 33973; plate!). NORTH CAROLINA: Swamp 1.5 mi. E. of Whiteville, Columbus Co. (*Schuster, Blomquist and Bryan,* 30001b, plate!; *Schuster and Blomquist* 29228).

Some of the plants listed above represent deviant phases and are discussed below, separately. In addition, some of the material reported in the literature (Frye and Clark, 1944; Redfearn, 1952; Kurz and Little, 1933) as *P. floridana* belongs here; I have also seen material collected and named by Schornherst, labelled *P. ludoviciana,* that is apparently referable here, but the material is so sparse a certain determination is impossible. Much of the material seen in the

Fig. 50.—*Plagiochila dubia* Gottsche. 1. Perianth-bearing shoot, the innovations cut off near base (x 11.5); 2. Robust shoot-sector, antical aspect (x 15); 3. Postical aspect of propaguliferous shoot (x 11.5); 4. Typical shoot-sector, postical aspect (x 11.5); 5. Sector of large shoot, lower portion, showing leaves with maximal basal dilation (x 11.5); 6-7. Female bracts (x 15); 8. Juvenile perianth in lateral aspect, dorsal keel at right (x 20); 9-10. Leaves (x 15); 11. Large underleaf (x 93); 12. Median cells with oil-bodies (x *ca.* 560). (Figs. 1-5 drawn to same scale; figs. 6-7, 9-10 drawn from same scale; all from *Schuster* 33324, Aspalaga Bluff, Florida.)

P. dubia-floridana complex, indeed, appears so impoverished that a certain determination is impossible.

The identity of our plants with some of the Central American and South American plants referred to as *P. dubia* is very questionable. For example, the plants from Costa Rica (Bozuca, *A. Tonduz* 15658; in herb. Yale), determined by Stephani, have much more remote leaves, a firmer, reddish-brown stem, and a more robust size than the most luxuriant Floridian plants. By contrast, the Bolivian plants ("Bergwald von Samaipata," 1600-1700 m., *Th. Herzog* 6109!), also determined by Stephani, probably belong here. These plants, for example, show the diagnostic development of propagula of the *antical* faces of the leaves, as well as the more copious, "normal" production of propagula of the postical leaf faces. A third collection, also in the herb. Yale, from Bolivia (Cordillera v. Sta. Cruz, *Th. Herzog* 3499) is of totally unrelated plants; the plants are dense-leaved, belong to the Crispatae, and are clearly allied to *P. blepharobasis* Herz. (see Herzog, 1932, p. 216). They possess much more longly decurrent postical leaf-bases than does that species, although the sharp dentition is confined to these decurrent bases; the postical leaf-margins are crispate much as in *P. undata*. These plants appear to represent an undescribed species.

Ecology.—In our area apparently common on shaded, but relatively dry coral limestone ledges. Associated there with various other Hepaticae, chiefly the Lejeuneaceae, *Lejeunea minutiloba, L. calcicola, Crossotolejeunea bermudiana,* and also *Dumortiera nepalensis* and *hirsuta,* as well as various tropical ferns (*Asplenium heterochroum, verrucundum, Goniopteris reptans,* etc.). The plant, in such sites, is relatively well-developed, shows a reasonable amount of pseudodichotomous branching, occasionally bears perianths, and freely develops propagula. The plants are always distinctly dentate-leaved, and correspond rather closely to the concept of *P. dubia* that can be derived from Gottsche's (1863) figures and diagnosis.

In addition to such calcicolous, robust plants, one finds two other types of plants which are referable evidently to *P. dubia,* partly as impoverished forms. Firstly, and most surely, are corticolous plants from northern Florida to North and South Carolina, found in wooded swamps along slow-moving coastal streams. Here they occur on the bark of *Nyssa aquatica, Planera aquatica* and other trees, associated with *Plagiochila undata, Metzgeria cf. myriopoda, Radula caloosiensis* (*cf. langloisii*), *Rectolejeunea maxonii,* and (in several stations) *Plagiochila yokogurensis fragilifolia.* At the North Carolina station, furthermore, are associated the orchid *Epidendrum conopseum* at its northernmost locality, and *Lopholejeunea muelleriana* at its northernmost locality. The corticolous swamp plants are somewhat less robust (2.8-3.4 mm wide), have uniformly unbranched aerial shoots, or rarely a single dichotomous fork, and are wholly sterile, although propaguliferous. They agree with the saxicolous phases of *P. dubia* in dentition (that of the South Carolina plants is, if anything, coarser than normal; that of the North Carolina plants less coarse than usual, but distinct), leaf-shape and oblique orientation, and in the vestigial underleaves. It appears wholly impossible to consider these plants as other than a strongly reduced phase of *P. dubia,* with which they agree

in the facies when dry (leaves only slightly deflexed, stems not or slightly arched). Clearly allied to the swamp plants alluded to above is material from the "Beech-Magnolia" type of Mixed Coastal Forest, as for example, plants from bark of Beech, ravine in Alum Bluff, Apalachicola River, Liberty Co., Florida (*Schuster* 33537; p.p., with *Plagiochila ludoviciana, Cheilolejeunea rigidula, Ceratolejeunea laete-fusca*).

Much less surely referable to *P. dubia* are even more reduced plants occurring in Florida, apparently exclusively in the southern third of the state. These have subentire to finely denticulate leaves that are often somewhat more imbricate, more dilated along the postical bases (which may be slightly shingled, frequently to the point where the stems, in postical aspect, almost "disappear" from view), and, in drying, have the simple aerial stems arcuate, almost terete in appearance, with the deflexed and tubularly convolute leaves erect and lying, in two lines, beneath the stem. The dry stems, as a consequence, are rigidly arcuate, and appear almost filiform! Associated with this, the plants in some cases tend to develop (with age) leaves that drop irregularly from the older portions of the axis. These plants, furthermore, tend to have the moist leaves suberect (Fig. 51:8), although occasionally more widely spreading (Fig. 51:9) on older axes. The few plants of this type seen have a weakly and remotely dentate perianth-mouth. Plants of this type appear restricted to the lower trunks of trees in evergreen hammock forests, where they occur on the bark of *Quercus virginiana, Citharexylem fruticosum,* and other trees. Associated are *Plagiochila ludoviciana, P. hypnoides, Ceratolejeunea laete-fusca, Cheilolejeunea* (*Euosmolejeunea*) *rigidula, Radula australis, Mastigolejeunea auriculata, Lopholejeunea subfusca,* and other *Lejeuneae,* and occasionally such ferns as *Polypodium plumula* and *Campyloneurum phyllitidis.* These plants, referred to a var. *integrifolia,* are discussed at length, below.

Differentiation.—*P. dubia* is distinguished by a most appropriate name. The species, in the existing literature, is not sharply separated from several species of the Sectio Hypnoides, and appears to be especially confused with *P. hypnoides* itself, as well as with its immediate relatives. The identification of the material from Florida with *P. dubia* rests upon comparison with plants from *Bolivia* (*Herzog* 3556!) and from Puerto Rico (*Pagan* 416!) and with the illustrations and descriptions of Gottsche (1863).

Three of the numbers cited above were also submitted to Dr. Th. Herzog, the eminent specialist on tropical Hepaticae. Dr. Herzog states: "Nach meiner Meinung könnten alle 3 als kleine Formen zu *P. dubia* L. et G. gerechnet werden. . . . Ihre Pflanzen sind etwas zwergig im Verhältniss zu der Abbildung bei Gottsche und, wie Sie sehen, auch zu den Exemplaren (Bolivia, *leg.* Herzog), die ich Ihnen beilege, und die von Stephani bestimmt wurden."

P. dubia is characterized essentially by the following ensemble of features: suberect to obliquely spreading leaves, rarely spreading as much as 75° from the stem, except on old shoot sectors; narrowly ovate-lingulate leaves, often with a very slight but characteristic sigmoid curvature (Figs. 49: 4; 50: 2); rather freely pseudodichotomous branching when mature; free propagulum production, with very often a few propagula produced from the distal portions of the antical face

—a most unusual feature; contiguous to slightly imbricate leaves, very short-decurrent postically, with the postical stem faces extensively exposed. The local material is often only questionably identifiable.

The Floridian plants differ, in part, in (a) less robust growth; (b)

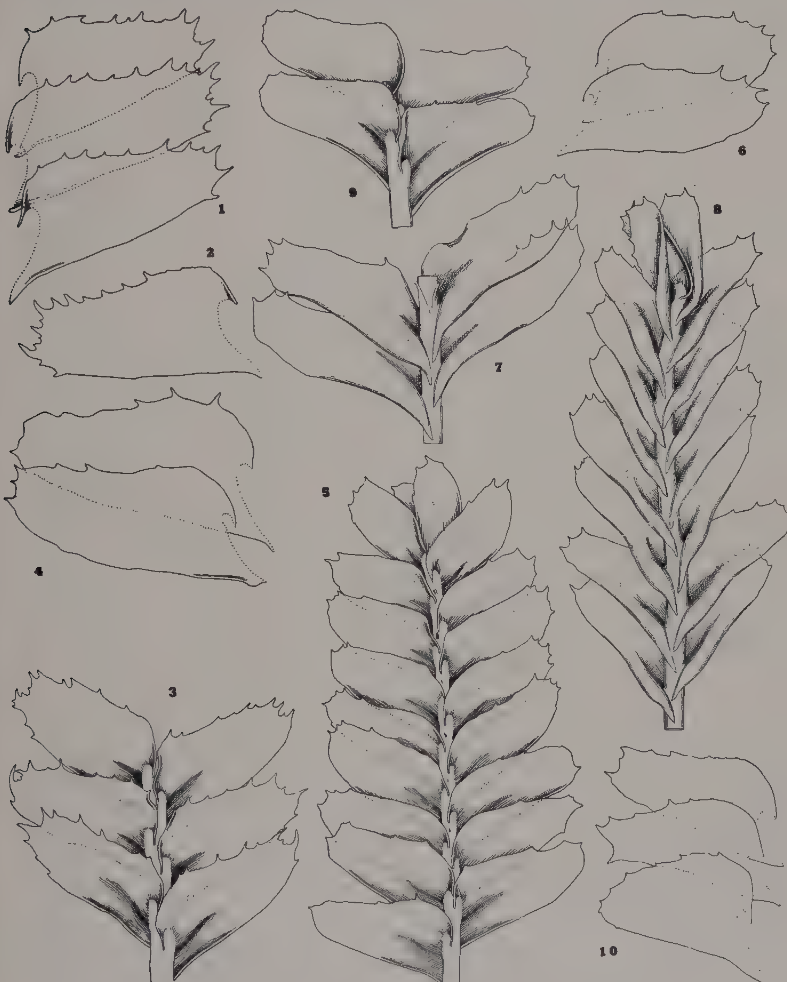

Fig. 51.—*Plagiochila dubia* Gottsche. 1-2, 4, 6, 10. Leaves (x 14.5); 3, 5. Shoot-sector, postical aspect (x 12.5); 7. Robust shoot-sector, antical aspect (x 12.5); 8. Shoot of extreme with erect-convolute leaves when dry, and subcircinate shoots (x 12.5); 9. Shoot of plant of type in Fig. 8, older portion, with patent leaves, postical aspect (x 12.5). (Figs. 1-2, 4, 6, 10, drawn to same scale; 3, 5, 7, 8-9 drawn to same scale; Figs. 1-3, *Schuster* 33973, Bamberg, South Carolina; 4-7, *Schuster* 30001b, Whiteville, North Carolina; 8-10, var. *integrifolia, Schuster* 19954b, Highland Hammock, Florida.)

nearly pure green color, with even the stem hardly brownish; (c) somewhat less strongly dentate leaves, with the teeth less sharp. These differences, as is seen under the discussion of *P. ludoviciana* (which undergoes very similar patterns of variation), are easily attributable to environmental causes. As with so many other tropical species, *P. dubia,* at the northern edges of its range, in Florida, is consistently less luxuriant than in the tropics.

The relationships with several members of both the Sectio Contiguae and the Sectio Hypnoides occurring in the West Indies, Mexico, and the Appalachian region are "uncomfortably" close.

My concepts of *P. hypnoides* are based partly on plants from the herb. Montagne, collected in Cuba (NYBG), on plants collected by Wright in Cuba (Hep. Cub. Wrightianae), on a series from South and Central America (leg. Herzog), as well as on the figures and discussion in Carl. *P. dubia* differs from *P. hypnoides* in several respects, principally in the lack of discrete underleaves and in the less imbricate as well as less dilated or ampliate postical bases of the leaves. The leaves, as a consequence, do not completely obscure the under surface of the stem on main stems, and the postical leaf-bases are not or slightly shingled. In *P. hypnoides* proper, the dilated postical leaf-bases, when *in situ,* extend across and often slightly beyond the stem. Correlated with this, the leaf in *P. hypnoides* is obliquely ovate-triangular in shape and tapers conspicuously from shortly above the base up to the narrowly subtruncate apex. Contrastingly, that of *P. dubia* is more nearly parallel-sided, and tapers slightly in the *distal half.*

These distinctions nearly or quite disappear in juvenile material. In *P. hypnoides, P. floridana* and *P. dubia* the upper leaves of shoots are always obliquely spreading or suberect (45-55, rarely 65° angle with stem apex); the juvenile leaves in all three species are often narrow, with the postical base not ampliate or only slightly so; as a consequence, the postical face of the stem is extensively exposed. The separation of such juvenile forms of the three species should not be attempted, since there does not appear to be any good basis for a definitive separation. Excellent examples of such juvenile forms are collections of *P. hypnoides* (presumably) from Brogdon Hammock, Dade Co., Florida (*Small and Mosier* 6232; Fig. 60), and from Palma Vista Hammock, Everglades National Park, Dade Co., Florida (*Schuster* 22148). The first of these was determined by A. W. Evans as *P. floridana* "probably." In the latter case, the upper, younger leaves are erect-spreading, and the shoot has a strongly "*P. floridana*-like" aspect.

Both *P. dubia* and *P. hypnoides* seem to have an almost equally extensive range in the coarseness of the teeth. In robust, coarsely dentate forms, the dentition may extend down along the postical margin to the dilated basal region. By contrast, more slender (usually shade) forms have lower, often subobtuse teeth, and the teeth are fewer and restricted to the distal one-third of the leaf. A valid distinction between the two species appears to lie in the degree of development of these teeth near the postical leaf-bases. In *P. hypnoides,* they always extend down to the decurrent postical bases of the leaves, and are

sharp and conspicuous there. In all forms of *P. dubia* seen they are obsolete or absent near the postical bases, becoming more distinctly developed in the distal two-thirds of the postical leaf-margins.

In the relatively narrow leaves, with the postical base only slightly dilated, *P. dubia* very closely approaches the southeastern *P. floridana* Evs. This similarity is enhanced by the fact that the upper halves of most shoots, in *P. dubia,* show oblique leaves (spreading at an angle of 45-55°). In fact, such shoots may show such a marked similarity that a separation of the two species sometimes appears almost impossible. This is particularly true of small, xeromorphic, phases. The similarity is enhanced by the close agreement in cell size and form of the oil-bodies. However, the mature, main stems of *P. dubia* show widely spreading leaves (65-75°), whose anterior (postical) margins generally lie nearly, if not quite at right angles to the stem. Juvenile or poorly developed plants of the two species appear virtually inseparable.

Part of the difficulty with respect to the identification of *P. dubia* is directly attributable to environmental causes. The xeromorphic, corticolous forms (such as a very small phase, only 1.8-2.2 mm wide, from the base of *Quercus virginiana,* in the drier portions of Highlands Hammock, *Schuster* 19954b) often have the leaves quite suberect, even on mature portions of shoots (Fig. 51:8), and are therefore extremely difficult to separate from the usually equally small *P. floridana.* However, even in such phases the leaves are more dilated postically (Fig. 51:9-10), particularly on the less mature, lower portions of shoots (Fig. 51:9). Such ovate-triangular leaves simply do not occur in normal *P. floridana.* Perhaps significant in the disposition of such xeromorphic forms is the difference in form of the oil-bodies, as contrasted to those of *P. floridana.* In *P. dubia* var. *integrifolia,* to which these small phases of *P. dubia* are here referred, usually 4-8, rarely 9, oil-bodies occur in the median cells, and these are very coarsely segmented, while in *P. floridana* there are 6-11, occasionally 12, oil-bodies per cell, and these are formed of smaller and more numerous segments (compare Fig. 53:6-8, with 53:1).

In addition to the disturbingly close relationship to *P. floridana* of the Coastal Plain, *P. dubia* exhibits unmistakable similarities to the Appalachian *P. virginica-caroliniana* complex. From this it differs in two principal ways: (a) the upper leaves are much more erect-spreading, at usually nearly a 45° angle with the stem; (b) mature shoots have the leaves, except the basal leaves of branches, non-falcate, clearly much more elongate, averaging 2.0-2.4 × as long as wide. In the *P. virginica-caroliniana* complex the upper and lower leaves, upon attaining their definitive size, are essentially similarly oriented and widely spreading; they also average much less than 2.0 × as long as wide under normal circumstances. In other respects (cell size; oil-bodies; dentition of the leaves; slightly decurrent and noncristate postical leaf-bases; vestigial underleaves) *P. dubia* may agree very closely with *P. virginica.* The very close affinity of *P. dubia* and *P. virginica* is particularly well brought out in corticolous plants, from Alum Bluff, Liberty Co., Florida (*Schuster* 33537). These plants have the sharply dentate leaves of *P. virginica,* with two of the terminal teeth often elaborated in a lobe-like fashion; they have the mature leaves widely

spreading (at an angle of 65-76°; with the postical margins at nearly right angles with the stem!); they have partly distinctly falcate leaves, with the dorsal base conspicuously long-decurrent. Yet the narrow leaf-form and the occasionally obliquely spreading leaves force one to consider them to be deviant *P. dubia*. The Alum Bluff plants occur with *P. ludoviciana*. It is noteworthy that, under the particular environmental conditions pertaining at this site, the *P. ludoviciana* is strongly chlorophyllose and deep green, the *P. dubia* is relatively pellucid and light green. In general, the latter "tends" to be a paler plant than the quite chlorophyllose, more opaque *P. ludoviciana* and *P. hypnoides*. Furthermore, the propagula, which occur in abundance, are found sparingly on the antical face of the distal halves of the leaves, as well as more abundantly on the postical (abaxial) faces, typical of *P. dubia;* in the wide range of plants of *P. virginica* seen, no antical propagula have been seen, although they possibly have been overlooked. It is possible that the Alum Bluff material (Fig. 49:8-16) represents an impoverished phase of the Mexican *Plagiochila acanthoda* Ldbg. et Gottsche, or of the Mexican plant called by Gottsche (1863) *P. chinantlana* var. *b*. Compare the figures here given for the Floridian plant with Gottsche (1863, pl. 5). Until more copious material becomes available, it appears best to retain the Floridian plant in *P. dubia,* although it forms a deviant element in that species. Note should also be taken of the fact that the Alum Bluff material shows close similarities in many respects to *P. intermedia* Ldbg. et Gottsche, *P. apicalis* Gottsche, and to a lesser extent to *P. expansa* Gottsche, species all described and illustrated by Gottsche. It appears certain that Gottsche was overly optimistic about the sharpness of some of the distinctions he utilized to separate these species, and that future study will demonstrate the need for synonymy in this complex. At such a time, the status of the present collection will need to be reinvestigated.

Variation.—As is evident from the preceding discussion, *P. dubia* appears to be a polymorphous plant, subject to wide latitudes in variation. It is possible the species is too broadly interpreted here, and that the plant which is subsequently segregated as var. *integrifolia* deserves separate specific rank. However, the limited number of collections from our area suggest that, for the time being, a conservative treatment is desirable.

The typical plant, as typified by the illustrations and description of Gottsche, and the plants from Aspalaga Bluff, Florida (*Schuster* 33324; see Fig. 50), is a robust plant, 3.5-4 mm broad. The plants most closely similar to those from Mexico, illustrated by Gottsche, are the Aspalaga Bluff plants (Fig. 50), which agree in size, in the shape, insertion, orientation and dentition of the leaves, in the shape and dentition of the female bracts (and in particular, in the irregularly spinose dentition, with the postical bases with several rather crowded teeth!), in the presence of a dorsal keel of the perianth, virtual lack of underleaves, and all other salient characters. Only the perianth mouth appears more irregularly and coarsely ciliate than in the Gottsche material. However, in the equally robust plants from the

"Devil's Millhopper," Gainesville, Florida (*Schuster* 33475a; Fig. 49: 1-7) and in plants from Gainesville, Florida (*N. L. T. Nelson* 57, 57A), the female bracts tend to be less sharply, and more regularly serrate-spinose, without the characteristic teeth of the postical leaf-bases, although the perianth mouth is more regularly, and less longly dentate with about 25-32 aciculate teeth per "lip" (and thus more closely approaches Gottsche's material); the perianth does not bear a dorsal keel, at least when juvenile. These two extremes, in the local plants, are bridged over completely by the equally robust material from the "Buzzard's Roost," W. of Gainesville, Fla. (*Schuster* 33416, etc.). In this material the bracts agree with those from the "Devil's Millhopper," i.e., are relatively moderately dentate, without spinose teeth near the postical base, as is the perianth mouth, which bears rather regular and rather numerous, relatively fine teeth. However, at least the antical base of the perianth is keeled, with the low keel elaborated at the juncture with the stem as a lamella. In this respect the plants closely approach those from Aspalaga Bluff. These three collections may be regarded as nearly typical of the species as any material from our region that has come to light. Until Mexican material becomes available, these plants may, indeed, be regarded as typical of the species.

Other aspects dealing with the variation in *P. dubia* have been previously dealt with above. The disposition of the troublesome small-leaved phases from the southern one-third of Florida, however, remains to be dealt with. These plants are perhaps best separated, at least tentatively, as follows:

P. dubia var. **integrifolia** var. n.
Figs. 51:8-10; 52; 53:6-8

Plantae multo minores quam *P. dubia;* virgae steriles 2.0-2.5 mm latae; caules plerumque simplices, sicci valde arcuati; folia sicca erecta, tubulo-convoluta, 1.55-1.75: 1; folii apex paene integer vel 2-3 dentibus parvis, inconspicuis praeditus; perianthii os paucis dentibus parvis, remotis, 2-3, raro 4-6 cellulas in longitudine praeditum. Typus: Highlands Hammock State Park, near Sebring, Florida (*Schuster* 26004 = *Schuster* 19954b); in herb. author.

Plants olive to brownish, rarely green, *much smaller,* 2.0-2.5 (on female shoots 2.8-3.0) mm wide. Leafy sterile aerial *stems simple,* usually scattered in occurrence (and not forming thick mats), *only* 8-16 *mm high,* arcuately spreading from substrate (vertical tree trunks), *strongly arcuate when dry,* (190) 200-235 μ in diameter. Leaves when *dry* $\pm$ *tubularly convolute, deflexed, lying erect in two juxtaposed lines beneath the stem,* when moist, erect-spreading (45-50°), to obliquely spreading (55-75°), *quite distinctly imbricate* (*in postical aspect, stem often nearly or quite hidden*), *narrowly ovate-triangular,* 1240-1360 μ *long* x 740-850 μ broad up to 1350-1625 μ long x 870-920 μ broad, only (1.45) *1.55-1.75* $\times$ *as long as wide;* apex rounded to rounded-truncate, *virtually edentate* or with 2-3 small to moderate, rarely coarse, teeth; *postical margin virtually edentate, or with 2-4 small and usually inconspicuous teeth.* Apical cells *ca.* 17-20 x 23-27 μ; median *ca.* 18-22 x 28-

35 μ; basal cells *ca.* 20-24 (26) x 29-38 μ; *trigones large,* but hardly confluent; intermediate thickenings occasional to frequent in cells of lower half of leaf; oil-bodies commonly only 2-4 to 5-6-segmented, the segments largely in a single row. *Propagula absent or usually only spar-*

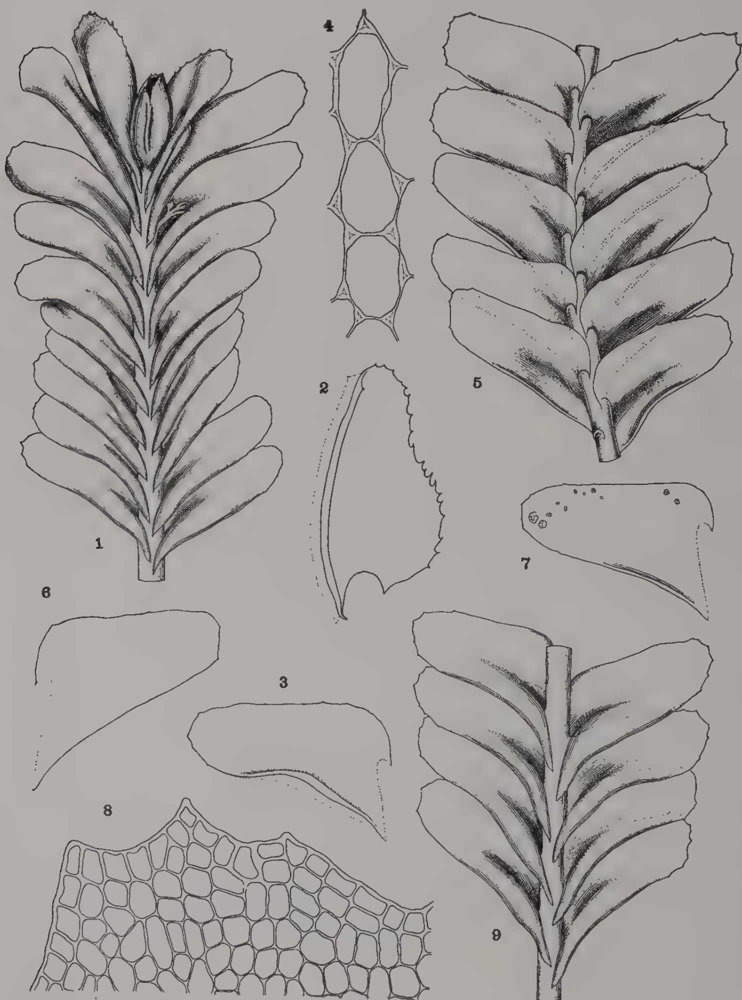

Fig. 52.—*Plagiochila dubia* var. *integrifolia* Schuster. 1. Plant with juvenile perianth (x 13.5); 2. Female bract (x 13.5); 3. Large leaf (x 13.5); 4. Median cells of base of leaf (x 410); 5. Part of shoot, postical aspect (x 19); 6-7. Leaves (x 16); 8. Apical cells of extremely dentate leaf-apex (x 160); 9. Shoot, dorsal view (x 16). (Figs. 1-3 from *Schuster* 22097, Long Pine Key, Florida; 4-9, *Schuster* 26004, Highland Hammock, Florida; for other figures of *Schuster* 26004 see Fig. 53:6-7.)

ingly developed, only on lower faces of leaves; *lower leaves sometimes tardily and irregularly breaking free,* but hardly caducous in the usual sense of that term.

Female bracts (from *Schuster* 22050, 22097) *ca.* 1950 μ long x 1175 μ broad, ovate-triangular, the postical margin above the *entire base with* 10-12 *or to* 15-16 *small, fine, relatively regular teeth* extending to and around the rounded apex. Perianth (juvenile; from *Schuster* 22050, 22097) with *few, small, distant teeth usually only 2-3, occasionally 4-6 cells long.*

Type.—Highlands Hammock State Park, near Sebring, Florida (*Schuster* 26004, 19954b), from bark of *Carya* and *Quercus virginiana,* p.p. (with *Plagiochila ludoviciana, Ceratolejeunea laete-fusca, Cheilolejeunea rigidula, Radula australis, Mastigolejeunea auriculata, Cololejeunea contractiloba,* etc., and the fern, *Campyloneurum phyllitidis*); *No.* 26004 may be considered the type (from this have been prepared Figs. 52:4-9 and 53:6-7).

Distribution.—Known only from a few collections from the southern third of Florida. Except for the type material, which is relatively copious, usually in small quantity and poorly developed, the collections from Collier-Seminole State Park, Collier Co. (*Schuster* 26179a; bark of *Xanthoxylum fagara,* with *Radula australis*), from Highlands Hammock, Highlands Co. (*Schuster* 19954b, 20106a, 26301, 26004, 26011a) and from the Long Key Pineland, Dade Co. (*Schuster* 22050, 22097) appear all referable to this extreme. The ecology of these plants has already been discussed; it is possible only an extreme environmental phase is at hand. However, the weakly dentate female bracts and perianth-mouth strongly suggest otherwise.

Discussion.—This plant is a small extreme, which may easily be confused by the beginner with juvenile phases of *P. hypnoides,* since it usually has the leaves so distinctly imbricate that the postical bases are shingled, thus hiding the stem from view (Fig. 51:9). The plant then belies its affinity with the Contiguae, and appears wholly different from "normal" *P. dubia.*

However, associated with such extremely dense-leaved plants one frequently finds individuals with somewhat less dense leaves, leaving the stem exposed to some extent, in postical aspect (Fig. 52:5). In either case, the plants differ from all phases of *P. hypnoides* in the vestigial underleaves and very weak or obsolete dentition, as well as in the non-cristate nature of the postical leaf-bases. It is possible that the plant deserves a higher taxonomic status than here accorded it. Although at first glance giving the impression of being a small, xeromorphic extreme of more "normal" *P. dubia,* such an interpretation seems an oversimplification. Although the Highlands Hammock material is partly from rather open hammock forests, on bark of trees such as *Carya* and *Quercus virginiana,* which frequent the less wet portions of hammock forests, the plants from Collier-Seminole and from the Long Key Pineland are from a very deep, evergreen type of hammock forest, of Caribbean affinity, as luxuriant and dense as can be found in Florida. Yet these plants are equally dense-leaved as the

Highlands Hammock material! The most robust material, to 2.8-3.0 mm wide on female plants, is that of *Schuster* 22050 (Long Key Pineland); it is also from the most shaded, humid site at which the variety has been found, yet is the densest-leaved of all the collections seen!

The collections from the stations referred here differ in minor respects from each other. For example, the material from Highlands Hammock (type; and *Schuster* 19954b, etc.) represents a strongly xeromorphic extreme, with a certain amount of brownish pigmentation, rarely exceeding 2.0 mm wide. The narrow leaves, somewhat dilated at the postical base, and the acute angle (40-45°) at which even the mature leaves spread, and the moderate size (*ca.* 2 mm wide) at once separate the plants from the accompanying *P. ludoviciana,* and place it near *P. floridana.* The plants bear a few propagula (while the accompanying *P. ludoviciana* is luxuriantly propaguliferous). In all foregoing features the plant approaches *P. floridana,* of the form with little spreading, suberect leaves. However, the older leaves of the plant show a marked tendency to be brittle and break off, even though there is no sharply marked caducous development such as we find in the *P. austini-sullivantii* complex (where even the young leaves may be caducous!). In the fragmenting of the leaves, the plants somewhat resemble *P. yokogurensis* subsp. *fragilifolia,* from which they differ at once in that only an irregular short stub (rather than the basal one-third to one-half) is left of the leaf, after fragmentation, in the suberect leaves, and in their scarcely dilated postical bases (as well as in the rare branching of aerial shoots, and in the much inferior size). Whether this tendency to lose the older leaves is widespread in the fo. *integrifolia* is impossible to tell at present. It has not been noted in more typical *P. dubia.* Loss of the older leaves is developed to a high degree in the scrappy plants from Juniper Springs, Florida (*Schuster* 31934, p.p. with *Radula caloosiensis* and *Cololejeunea contractiloba*). These plants are as small as in var. *integrifolia,* but bear the strong teeth of normal *P. dubia.* The plants are wholly deviant, and appear impossible to refer safely to any species except *P. dubia.*

The material from the third locality referred to above, from the Long Key Pineland (*Schuster* 22097, 22050) is from a much more mesic site, from dead lianas and roots in deep hammock forest; it shows even more reduced dentition, wholly lacks propagula, and has a slightly different facies. The larger plants (to 2.8-3.0 mm wide) are strongly dense-leaved, with the facies of a small, virtually edentate *P. hypnoides,* which they also resemble in that the leaves, when dry, are little convolute, and spread to some extent (rather than being erect and appressed to the stem, as in the type material). These plants, particularly those of *Schuster* 22050, give perhaps the best idea of the mature state of this variant. They also suggest strongly that the var. *integrifolia* is possibly a wholly distinct species, since (a) the admittedly juvenile perianths bear much shorter teeth at the apex, many of which terminate in slime papillae; the teeth are mostly 2-4 cells long, only a few attaining a length of 5-6 cells; (b) the perianths lack an antical wing; (c) the female bracts are weakly serrate-dentate, rather than irregularly spinose-dentate. The position of the gynoecia is identical with that typical of *P. dubia* s. str.: the leading axes either have gynoecia at the apex, which may develop two subfloral innovations, which are almost immediately again fertile; or, the leading axis forks pseudo-dichotomously, and each of the forks is almost immediately fertile, bearing usually each a single subfloral innovation, which may soon again be fertile. In either case, there is a tendency for clustered, sympodial gynoecia, with all but the original one that terminated a main axis situated on very short branches.

Although these plants are closely similar to juvenile *P. hypnoides,* they are clearly distinct in the generally less widely spreading leaves (postical margins only occasionally approaching a right angle with the stem), the vestigial underleaves, and the edentate basal portions of the leaves. The plants also exhibit some similarity to *P. floridana,* particularly in: the leaves on robust female shoots being largely at an angle of 45-55° with the stem (but on less robust sterile shoots often spreading more widely). The plants are of about the same size, sterile shoots attaining a width of 2.5-2.6 mm, female shoots of 2.8-3.0 mm. The underleaves are also equally minute to vestigial. The postical leaf-margin is equally short-decurrent. The resemblance to *P. floridana* ceases at this point, and the plant differs as follows: (1) Lateral leaves typically almost edentate, with at most 2-4 vestigial low teeth 1, rarely 2 cells high (coarsely dentate in typical *floridana,* at least near the leaf-apex). (2) Leaves narrowly ovate-rectangular and somewhat narrowed from base to apex, the subbasal width to *ca.* 920 μ, the length to *ca.* 1625 μ; *e.g.,* length distinctly less than twice the width (in typical *floridana,* leaf-length *ca.* 2-2.4 × the width, the leaf-shape nearly rectangular, little or scarcely dilated at postical base). (3) Female bracts narrowly ovate, rather distinctly dilated on basal half of postical margin, quite finely dentate with teeth rarely over three cells long (in typical *floridana* with postical margin little arching, the shape essentially subrectangular, the apex and postical margin with few coarse, spinose teeth). (4) Perianth-mouth with few, small teeth only 1-3 cells long (closely spinose-ciliate at mouth in typical *floridana*). (5) Juvenile leaves scarcely longer than wide to 1.4 × as long as wide, varying from short-ovate to slightly obovate, entire (bilobed or spinose-dentate and at least 1.5 × as long as wide in typical *floridana*).

PLAGIOCHILA FLORIDANA Evans
Figs. 53:1-5; 54-55A

Plagiochila floridana Evans, Bot. Gaz. 21:190, 1896.

Plants in green to brownish-green patches, with a sharp division into radicellose reduced-leaved, rhizomatous creeping stems and leafy aerial stems that stand away from their substrate. Leafy shoots usually 2.4-2.8, occasionally 3.0-3.2 mm wide x 10-15 (25) mm long. Stems firm, yellowish-brown, rather slender, *ca.* 180-225, occasionally 250 μ thick; branches few, diffuse, monopodial on weak shoots, but on robust shoots the *Frullania*-type branches nearly as vigorous as the stems, then *becoming pseudodichotomous;* gynoecia almost always with 2 subfloral innovations, appearing situated in the fork of a dichotomy. Leaves slightly to distinctly imbricated, horizontally *erect-spreading (at an angle of* 40-50° *on the upper portions of shoots, and usually even on mature shoots;* with age often more widely spreading, to an angle of 55-65°), *narrowly oblong to ovate-rectangular and not or hardly falcate* when mature, *sometimes almost rectangular* or weakly rectangular-falcate, from *ca.* 400 μ wide x 1100 μ long (type) to 520-530 μ wide x 1150-1200 μ long, occasionally 570-700 (800) μ wide x 1350-1550 (1620) μ long, rarely broader and only 575 μ x 1150 μ long (*length usually* 2.0-2.4, occasionally 2.2-2.5 × the width); leaf-insertion rather narrow, usually 0.85-0.9 the maximal leaf-width (*ca.* 480 μ when leaf is 520-530 μ wide), the *postical leaf-base short-decurrent, the antical leaf-base only moderately decurrent; antical margin nearly*

straight to slightly concavely arched, strongly reflexed for 0.6-0.9 its length, the cnemis a distinct narrow dorsal fold; median part of leaf depressed and broadly and shallowly sulcate-depressed for *ca.* 1/3 its length; *postical margin scarcely to slightly dilated above the base* and

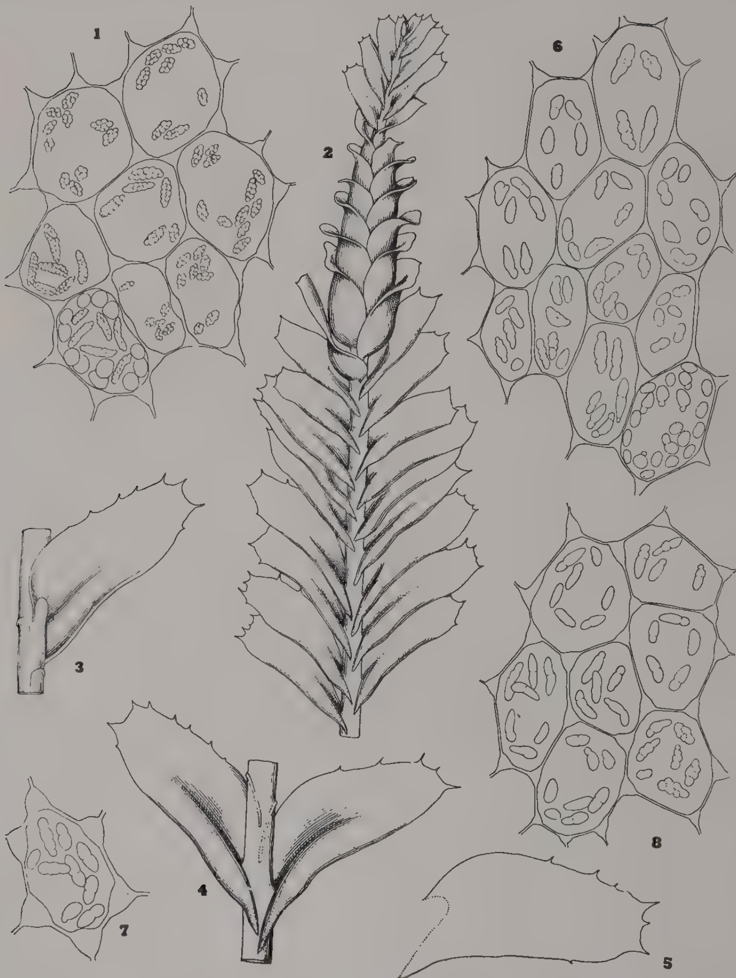

Fig. 53.—*Plagiochila floridana* Evs. 1. Median cells with oil-bodies (x 500); 2. Male plant, antical aspect (x 13); 3. Leaf, *in situ,* postical view (x 17); 4. Shoot-sector, antical aspect (x 17); 5. Leaf (x 17). *Plagiochila dubia* var. *integrifolia* Schuster. 6. Cells of leaf-middle, the lowermost with chloroplasts as well as oil-bodies drawn in (x 485); 7. Cell of mod. *pachyderma,* with oil-bodies (x 540); 8. Cells with oil-bodies (x 460). (Figs. 1-5, from *Schuster* 26013a; 6-7, *Schuster* 26004; 8, *Schuster* 26011a; all from plants from Highlands Hammock, Florida.)

arched, but distal two-thirds of margin virtually straight and *subparallel or only slightly converging to the antical margin,* the leaf thus often appearing nearly rectangular; *leaf-apex usually subtruncate, often appearing sharply but shallowly bilobed,* at other times 3-4 dentate; postical margin with occasionally 1-2, but more often usually 3-5 small, spinose, irregular teeth (the leaf-margin as a whole with 6-10 teeth, only juvenile leaves merely bilobed or bidentate; *apical two lobe-like teeth often characteristically divaricate*). Cells thin to moderately thick-walled, with small and concave to rather large, subconfluent trigones, the walls generally lacking intermediate thickenings; marginal cells in 1, rarely 2 rows somewhat to distinctly thick-walled and often forming a slight border (the tangential walls often rather distinctly irregularly, undulately thickened); cells at base of apical teeth usually 25-27 μ long along margin; cells along middle of postical margin variable, *ca.* 22-25 to 36-43 μ long x (13) 15-17 μ wide, often quite elongate and narrow, often thick-walled; marginal cells of postical base somewhat more elongate, usually distinctly thick-walled; cells of leaf-tip *ca.* 18-21 x (20) 22-29 μ, of leaf-middle *ca.* (17) 18-24 x 24-36 μ; basal cells of midline of leaf 22-25 (27) x 32-45 μ, not forming a vitta; trigones distinct, but usually quite concave-sided, in robust phases often large and bulging, the longitudinal intervening walls thickened, the cells thus appearing seriately thickened in longitudinal lines; oil-bodies 6-11 (12) per median cell, 3 x 5-8 (9) μ, a few to 3-3.5 x 10 μ, distinctly segmented of globules *ca.* 0.8-1.5 μ, usually arranged in 2 (-3) rows; chloroplasts 4.5-5 μ. *Underleaves minute,* usually lanceolate or of 2-several uniseriate cilia to lanceolate-ciliate, the segments commonly terminating in clavate slime-papillae. Asexual reproduction commonly present, by means of *leafy propagula of the postical (often also of the antical) leaf-surface.*

Dioecious. Male plants to 2.4 mm wide; androecia somewhat whitish-green, contrasted to the darker remainder of the plant, formed of 6-11 pairs of closely imbricate, ventricose bracts, which are erect (except for the distal 0.15-0.25, which is erect-spreading or spreading, or occasionally even reflexed); concave basal portions of bracts quite entire both dorsally and ventrally, the free, spreading portions varying from truncate to rounded and subentire to obscurely emarginate, or bidentate, with ill-defined teeth; bracts to 1200 μ long in basal portion of androecium, becoming progressively smaller distally, the compactly spicate androecium thus distinctly tapering, proliferating vegetatively distally. Female inflorescence at apex of main leafy shoots, usually eventually subtended by 2 (less often 1) innovations. Female bracts like leaves, but postical base more dilated, ovate-rectangular to subrectangular, 1000-1025 μ wide above base x 1750-1950 μ long, the entire *postical margin to the base coarsely spinose-dentate with ca.* 8-11 *teeth, the apex with* 3-5 *coarse spinose teeth.* Perianth (immature) broadly campanulate in lateral outline, wider than long, *not or obscurely winged, the two keels subequal; mouth longly, closely coarsely ciliate.* Mature (but sterile) perianth with bracts sheathing at base,

suberect to widely spreading, the perianth quite obvious, in dorsal profile ovoid, widest in basal third, to 1000 μ wide below x 1800-2000 μ long (in lateral profile widest near apex, the antical and postical "keels" subequal, *ca.* 1200 μ wide near the rounded-truncate apex); postical

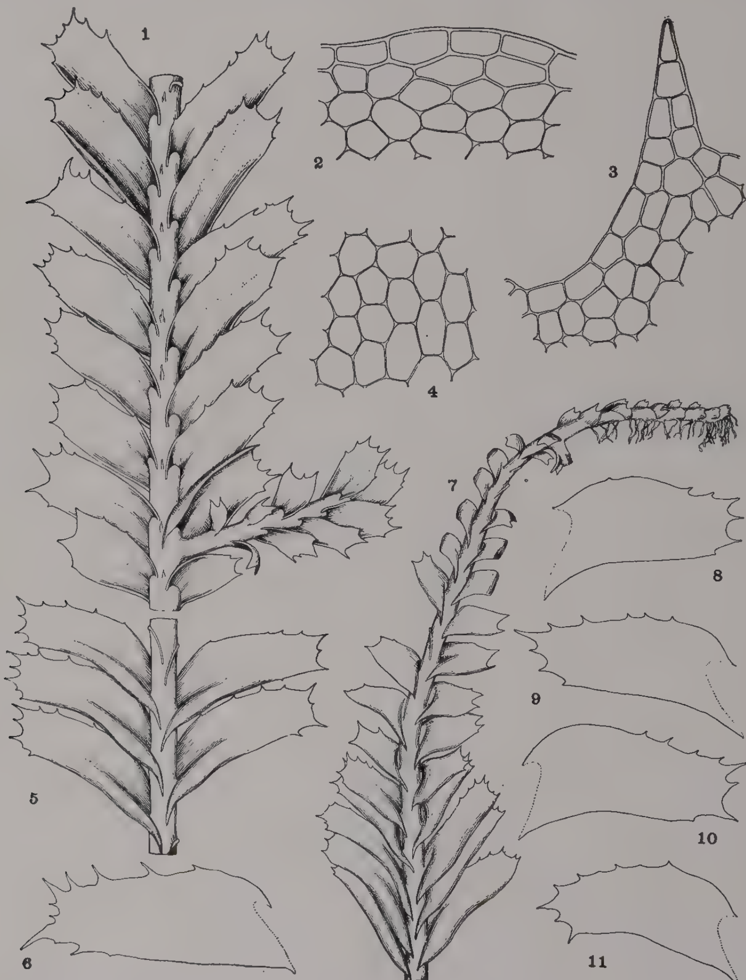

Fig. 54. *Plagiochila floridana* Evs. 1. Shoot-sector, postical aspect (x *ca.* 16); 2. Cells of middle of postical margin (x 205); 3. Cells of leaf-apex (x 205); 4. Median cells (x 205); 5. Part of robust shoot, antical aspect (x 14); 6. Leaf (x 19); 7. Apex of shoot with decumbent, rhizoidous apex (x 14); 8-11. Leaves (8-9, x 19; 10, x 21; 11, x 18). (Fig. 1, from type specimen; 2-5, 7-11, from specimen collected by Rapp, issued in Verdoorn's Hep. Select. et Crit. No. 386; 6, from plants collected at Alexander Springs, Florida, illustrated in Fig. 55.)

keel not carinate, antical keel weakly carinate in basal one-third to one-fourth, the keel edentate, but sometimes proliferated as a lobe-like wing at base of perianth or at juncture with axis; *mouth ciliate with spinose teeth 2-3 cells wide at base, terminated in up to 5-7 superimposed cells;* terminal cells spinose, tapering, *ca.* 15-19 x 32-46 μ, the uniseriate cell-row below formed of cells *ca.* 18-25 μ long x 20-22 μ broad.

Type.—Ocala, Florida (*L. M. Underwood;* Underwood and Cook, Hep. Amer. No. 109, sub *P. ludoviciana!*).

Variation.—*P. floridana* is apparently one of the less variable species among our *Plagiochila* flora. The above description is based on the type material, on a specimen collected at Sanford, Fla., by Rapp (distributed *in* Verdoorn, Hep. Select. et Crit. No. 386), on male plants (*Schuster* 26013a) from Highlands Hammock and on perianth-bearing plants from Alexander Springs (*Schuster* 31519). However, the variation in a) leaf-shape, b) leaf-orientation, c) dentition of the leaves, d) form and dentition of the female bracts, appears to be so considerable that some discussion appears necessary. To some degree, at least, the variation is probably the result of genetic differences.

Leaf-shape.—This is typically so rectangular that it closely simulates that of *P. diffusa.* However, the more coarsely dentate leaf, often bilobed at the apex, and the suberect leaves, as well as essentially immarginate leaves separate such material from *P. diffusa.*

In material such as the Rapp specimen (Verdoorn's No. 386), the leaves are slightly more dilated basally, and distinctly narrowly ovate-rectangular to ovate-falcate (Fig. 55A:5-7), but are dentate much as in the type (even though the terminal two coarse teeth are only exceptionally divergent). The Rapp material, on the basis of the sometimes less erect leaves, and the somewhat dilated postical bases, is perhaps related to *P. dubia.*

In closely allied plants referred to *P. dubia* the leaves become more ovate-falcate to ovate-rectangular, with a rounded apex and virtually entire margins (Figs. 49:4-5; 50:1-4, 9-10). Such plants are perhaps not specifically distinct, but depart so widely from the typical concept of *P. floridana* that it appears impossible to retain them in *P. floridana.* Unfortunately, a certain amount of transition in shape and dentition occurs.

Leaf-orientation.—Typically, *P. floridana* has the leaves of both the terminal portions of shoots, as well as older, mature leaves, spreading on each side at an acute angle (commonly 40-45°) from the stem-apex; this is well-illustrated in Fig. 54:1, from the type specimen, and in both the male and female plants illustrated (Figs. 53:2-4; 55:1, 5, 8).

However, much material shows only the upper leaves with the angle retaining the acute form (as in the Rapp specimen Fig. 54:5, 7), while the mature lower portions of shoots show the leaves widely spreading laterally (at an angle as high as 60-65°, as in Fig. 54:5, also drawn from the Rapp material).

In the subentire-leaved plants referred to *P. dubia* the angle again varies from *ca.* 48-50° to as high as 65°. Since the various keys (Evans, 1896; Frye and Clark, 1944) emphasize this as *the* differential feature of the species, it is evident that the determination of this species has been a source of considerable difficulty.

Dentition.—Typically the leaves are coarsely dentate with relatively irregu-

lar teeth (Figs. 54:1; 55:9-10); this is equally true of the Rapp material (Fig. 54:6-11), and of the male and female plants referred to the species (Figs. 53:3-5; 55:9-10). In several specimens, referred to the allied *P. dubia* (Fig. 51:8-10), the denticulation is obsolete or rather reduced, giving the plants a strongly deviant appearance. The Mississippi plants (Fig. 55A:1-4) are clearly transitional.

Denticulation of bracts.—Typically the bracts are ovate-rectangular with (6) 8-11 coarse to fine, spinose, strongly irregular teeth on the postical margin which point in varying directions (Fig. 55:6-7). In the allied *P. dubia* the often more strongly ovate bracts may bear smaller, more regular marginal teeth always more numerous (10-16 or more on the postical margin), and the denticulate apex is sometimes rounded (Fig. 52:1-2). As is evident from Fig. 50:6-7 *P. dubia* may have almost as coarse, although more numerous, teeth.

Unfortunately, there appears to be considerable diversity in the number and degree to which the teeth of the bracts are developed. In the type material, figured by Evans, the bracts are relatively short and rectangulate in shape; they bear a number of very coarse, spinose teeth on the distal halves and at the apex (usually 6-7 per bract), and several smaller teeth near the postical base. In the otherwise typical plants from Alexander Springs (Fig. 55:6-7) the bracts are more elongate, bear more numerous, less polymorphous, and generally less coarse teeth. The range of variation in this respect, however, is not great enough in available material to afford a total transition to the condition typical of *P. dubia.*

Development of collenchyma.—Typically, *P. floridana* has slight to hardly thickened cell-walls, except in the 1-2 rows of marginal cells, where the tangential walls are often rather considerably thickened, and has small to moderate trigones that do not bulge into the cell-lumen. However, much of the material shows coarse trigones, often somewhat ill-defined, that distinctly bulge into the cell-lumen. Associated, in extreme cases, the longitudinal cell-walls may be very considerably thickened, and rare intermediate thickenings develop.

The preceding outline suggests that the pattern of variability in *P. floridana* centers largely around a "normal" and "typical" extreme, with uniformly suberect leaves; coarse dentition; narrowly rectangulate, parallel-sided leaves whose postical bases are not or hardly dilated; female bracts with a limited number of coarse teeth, and an ovate-rectangulate to oblong shape; perianths with a closely spinose-ciliate mouth. The pattern of variation extends from this type to one with the older leaves more widely divergent, with a finer dentition and more or less rounded leaf apices; with narrowly ovate-rectangular leaves, whose postical bases are perceptibly dilated; female bracts with weaker dentition and a distinctly narrowly ovate shape; perianth with short, small and usually distant teeth. Plants with the latter series of characters fully expressed appear identical to the small phases of *P. dubia,* to which they are tentatively referred.

Male Plant.—The male sex of this species has been hitherto unknown. Since the female sex is known, this then becomes one of three regional species, known from both sexes.

The male plants (*Schuster* 26013a, Highlands Hammock, Fla.) are *ca.* 2.4 mm wide, thus subequal in robustness to the female plants. The androecia are more whitish-green in appearance than the rest of the plant, and are formed of 6-11 pairs of closely imbricate bracts, which

are ventricose and erect, except for the distal one-fourth to one-sixth (which is erect-spreading to spreading or occasionally even reflexed), the concave basal portion of the bracts are quite entire-margined, both dorsally and ventrally, while the free, spreading portion of the bract varies (in the single collection available) from rounded to subtruncate

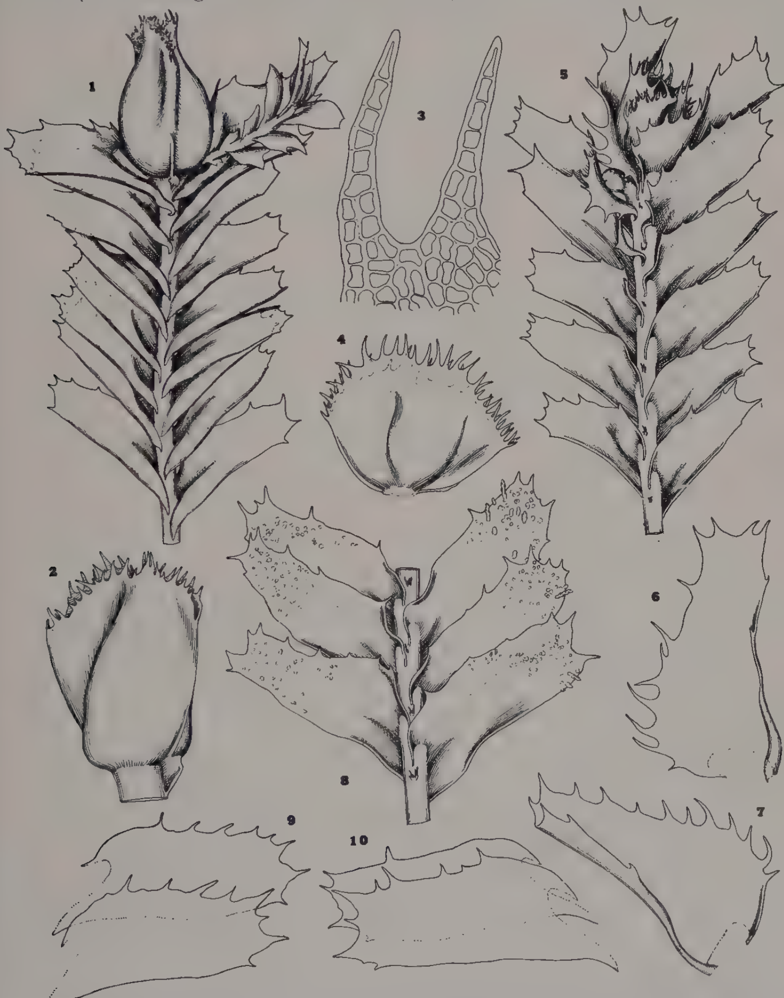

Fig. 55.—*Plagiochila floridana* Evs. 1. Perianth-bearing shoot, one innovation cut off at base (x 14); 2. Perianth, lateral aspect, antical keel at right (x 17); 3. Teeth of perianth-mouth (x 150); 4. Juvenile perianth (x 17); 5. Shoot apex with juvenile perianth, postical aspect, with one immature innovation (x 14); 6, 7. Bracts (x 17); 8. Sterile, propaguliferous shoot-sector, postical aspect (x 17); 9-10. Leaves (x 17). (All drawn from plants from Alexander Springs, Florida, *Schuster*.)

and subentire to obscurely emarginate or retuse (with rounded or obtuse, shallow lobes), to very obscurely bidentate, with ill-marked teeth. The male bracts are up to 1200 μ long, in the basal portion of the androecium, but become progressively smaller distally. As a consequence, the compactly spicate androecium tapers distally. Although terminal

Fig. 55A.—*Plagiochila floridana* Evs. grading into *P. dubia* Gottsche. 1. Shoot-sector, with furcate branching and two gynoecia (x 6); 2-3. Shoot-sectors, in postical and antical aspect, in 3 with unusually large, atypical underleaf (x 18); 4. Leaf and large underleaf, *in situ* (x 18); 5. Leaf (x 10); 6. Shoot-sector, postical aspect (x 10); 7. Leaf with propagula (x 10); 8. Two leaves (x 16); 9. Shoot-sector, postical aspect (x 11.5); 10. Juvenile perianth, lateral view (x 18). (Figs. 1-4 from Mt. Olive, Miss., *Schuster;* 5-7, from Sanford, Fla., *Rapp,* Dec. 1903 (NYBG); 8-10, from *Webster and Wilbur* 756, Mississippi.)

at first, the apex of the androecium proliferates in all examined cases, forming a new vegetative shoot, whose basal 3-4 pairs of leaves are smaller than normal, merely 1-3-dentate at the apex.

In the virtually entire-margined male bracts, *P. floridana* exhibits a similarity to many other species of the genus, in which the male bracts are less dentate than the vegetative leaves. In the present case, the vegetative leaves are distinctly dentate with sharp, if not excessively salient teeth. The androecial region, as a whole, varies from 2.4-4.0 mm in length.

Distribution.—Evidently a local and rather rare species, found in Florida largely in the central, "Oligocene Island" region, and to the north, and extending westward along the Gulf Coastal Plain to Mississippi and probably Louisiana. The range of the species northward and westward from Florida is uncertain since in the Coastal Plain from Georgia to North Carolina, and from Mississippi to Louisiana, all the material in this complex appears rather poorly developed and is either transitional to *P. dubia,* or better referred to the latter.

The species appears to be confined to "old" areas in the Coastal Plain; in Florida chiefly found in the "Oligocene Island" area, where so many "old tropical" species occur; on the Gulf Coastal Plain found in the relict station for *Trichomanis petersii* (Mississippi) and in the rich "Beech-Magnolia" Forests, on *Magnolia grandiflora,* associated with *Halesia diptera, Illicium floridanum, Ilex opaca,* etc. (Mississippi; see Schuster, 1954).

FLORIDA: Alexander Springs, Ocala National Forest, Lake Co., c. perianth (*Schuster* 31519); Monroe, Seminole Co. (*Rapp, Jan. 1934;* issued as No. 386 in Verdoorn's Hep. Select. et Crit., and erroneously labeled as from "regione originali"); "Balanced Rock," edge of Chipola R. flood-plain, 7 mi. NE. of Mariana (*Kurz* 148! mixed with *Cololejeunea ornata;* plants less dentate than typical *P. floridana,* but with subtruncate leaf-apices); near Oviedo (*Rapp* 85! with antical as well as postical propagula; with *P. hypnoides*); below Juniper Springs, along Juniper Creek, Ocala National Forest, Marion Co. (*Schuster* 33460, *c. per., c. propagula; Schuster* 33454, *c. propagula*); Hardaway Tract, Liberty Co. (*Schornherst* 314!); Hillsborough River State Park, Hillsborough Co. (*Schuster* 22853a, 33905a, male). Highlands Hammock State Park, W. of Sebring, Highlands Co. (*Schuster* 26013a, male). [Also reported from Collier, Dade, Polk and Seminole Cos. (*fide* Redfearn, 1952) and Apalachicola R. bluffs (*Schornherst,* 1939); Mariana, Jackson Co. (*McFarlin,* 1934); Sanford (*Rapp,* Dec. 1903!; *No.* 30!; Rapp, 1934); Suwannee R. in Suwannee Co. (*Schornherst,* 1939); *fide* Frye and Clark (1944). These reports wholly unreliable, except for the Rapp material.] MISSISSIPPI: *Trichomanis petersii* locality, near Mt. Olive (*Schuster,* Aug. 1951; plate); De Soto National Forest, W. of Hwy. 49, *ca.* 14 mi. N. of Gulfport, along Big Biloxi R. (*Webster and Wilbur* 756 p.p., with *Rectolejeunea maxonii*). CUBA: Sierra de las Yuguas, San Diego de los Banos, Pinar del Rio (*Br. Leon* 5241; questionable material, with androecia, referred to *P. ludoviciana* by Evans; NYBG).

In addition to the preceding material, the following are somewhat doubtful plants, provisionally referred to *P. dubia,* which deserve future study in connection with the limits of *P. floridana.*

NORTH CAROLINA: Swamp, 1.5 mi. E. of Whiteville, Columbus Co., N. of

Rte. 74-76 (*Schuster and Blomquist* 29228; *Schuster, Blomquist and Bryan* 30001b). SOUTH CAROLINA: Wooded swamp, 8 mi. S. of Bamberg, off U. S. Hwy. 301, Bamberg Co. (*Schuster* 33973, 33982).

I have also seen juvenile material from Florida, attributed to *P. floridana* by Evans (in herb. Yale), which I regard as not safely determinable, from Lena Stein Ravine, 3 mi. NW. of Tallahassee (*Kurz* 9!) and from Cross City (*Kurz* 232!).

Ecology.—In Florida chiefly found in deep, partially evergreen swamp forests, and in rich hammock forests, where the species occurs at the bases of tree trunks and on exposed roots, sometimes on the exposed knees of *Taxodium distichum* (and then barely above the flooding level). Associated are *Ceratolejeunea laete-fusca, Cheilolejeunea rigidula, C. clausa, Lopholejeunea subfusca,* and other Lejeuneae. The species appears confined largely to mesic sites near standing water, where the humidity is permanently high. Less often it is found over coral limestone, and soil over it, along rivers (such as the Hillsborough River, in Florida), associated with *Plagiochila ludoviciana* and *Lejeunea floridana.*

In the few stations situated outside of Florida, found (in *Schuster* 19167a, from near Mt. Olive, Miss.) over damp, shaded ledges, with *Trichomanis petersii, Lejeunea flava* and *Lejeunea* cf. *minutiloba;* and on the bark of *Magnolia grandiflora, in* "Beech-Magnolia" forest along the Big Biloxi River (*Webster and Wilbur* 756), associated with *Metzgeria myriopoda, Rectolejeunea maxonii, Radula caloosiensis* (*cf. langloisii*).

The plant rarely occurs in any quantity, occasionally occurs as scattered plants, which then develop isolated, arching, simple or hardly ramified, leafy aerial shoots. The latter, in drying, have deflexed leaves and become characteristically slender and arcuate. Less often, and only under optimal conditions on the bases of trees in swamps, forming large, olive-green to olive-brown patches (and then frequently fertile). Propagula appear to be developed in almost all collections seen, even though Frye and Clark state "gemmae unknown." The propagula occur both on the postical face of the distal halves of the leaves, and near the posterior margins of the antical (adaxial) faces. The very frequent occurrence of propagula in the latter position appears to be an important systematic criterion, since in our other species it occurs, and there rather rarely, only in *P. dubia* and *P. ludoviciana.*

Differentiation.—*P. floridana* is characterized by an ensemble of characters, of which the most important are: (a) the inability to develop a mod. *laxifolia,* the leaves therefore always being slightly to distinctly imbricate; (b) short decurrent postical and antical leaf-bases; (c) oblong-lingulate, virtually parallel-sided leaves, averaging at least twice as long as broad; (d) propagula usually developed, on both postical and antical leaf-faces; (e) the very diagnostically suberect to oblique orientation of the narrow leaves. The latter criterion gives the plants an aspect that is wholly deviant, only the very closely allied *P. dubia* sharing a similar orientation of the leaves.

P. floridana was confused by Underwood with *P. ludoviciana,* and is compared by its author with this species. However, it differs from it not only in the inferior size, the narrower, hardly ovate-falcate leaves, which are nearly parallel-sided for their distal two-thirds, in their shorter leaf-insertion, with the dorsal base rather short-decurrent, the postical base quite short-decurrent and never strongly reflexed. In the field, furthermore, the fact that the leaves never have the postical margin at more than a 65-75° angle with the stem at once separates this much smaller species from *P. ludoviciana* (in which the postical leaf-margin is characteristically at a right angle with the stem). No close relationship between the two can be hypothesized.

Among our other species, confusion is perhaps possible, on account of the narrow and elongate leaves, with *P. austini,* to which the species is not at all closely related. The two, however, share some features (1) evidently elongate, parallel-sided leaves; (2) short decurrence of postical base; (3) cell form and size; (4) form of the leaf-apex, which is often coarsely bidentate or bilobed; (5) plant size. This superficial similarity has resulted in confusion of the species by Stephani, who determined material of this species as *P. sullivantii* St. (nec Gottsche) (= *P. austini* Evs.), from Sanford, Fla., Rapp, Dec. 1903, NYBG. In spite of the superficial similarities, the two species differ not only in mode of reproduction (leafy propagula in *P. floridana vs.* caducous leaves in *P. austini*), but in color and in the suberect leaves of *P. floridana. P. floridana* also never shows the very strong tendency present in *P. austini* to produce narrow, largely 2-lobed leaves, devoid of accessory teeth, on less robust shoots or branches.

This occasional difficulty in separating the species is clear when such plants as Rapp's material (Sanford, Fla., Dec. 1903) is examined. The mature, robust shoots here bear large leaves, *ca.* 2.25 mm long, which spread at an angle of 65-70° (Fig. 54:5). Although, on the basis of size and spreading of leaves, these might be sought under *P. diffusa,* they lack the obvious border of the leaves of that species, have somewhat ovate-lingulate leaves, with slightly expanded postical bases, and more decurrent antical bases. (In the key in Frye and Clark, such plants would key to *P. smallii* = *diffusa,* on the basis of the robust size, to 4.5 mm wide; however, size here appears to be no criterion.) These specimens possess leafy propagula of both leaf-surfaces — at once eliminating *P. austini* from consideration.

Evans (*loc. cit.,* p. 191) also compares *P. floridana* with *P. dubia* Lindenb. and Gottsche. He states that the former is "near" the latter. *P. dubia,* judging from a specimen from Puerto Rico (Laguna San José, Rio Piedros, Aug. 6, 1937, F. M. Pagan) typically differs in the more robust size, the narrowly, obliquely ovate leaves, whose postical margin is somewhat arched and expanded basally (and thus with the leaves gradually but slightly narrowed distally, rather than nearly parallel-sided), as well as in the smaller marginal teeth, all of which are subequal in size (*i.e.,* none of the leaves shortly bilobed distally). Judging from the drawings in Stephani's unpublished Icones, and from the Pagan specimen, there is little immediate relationship between typical *P. dubia* and *P. floridana.*

However, in the southeastern United States occur plants which appear to represent a small, somewhat impoverished and atypical phase of *P. dubia* (see discussion under the latter). These plants almost fully intergrade with *P. floridana,* and quite confirm the opinion of

Evans about the close affinity of the two taxa. Indeed, prolonged study has not revealed any firm and final criteria which always serve to separate the two taxa, in our area. The retention of *P. floridana* as a species distinct from *P. dubia* is predicated on two assumptions: (a) the constellation of characters of the two species are such that although "individual characters intergrade," the taxa themselves do not wholly intergrade; (b) the regional material referred to *P. dubia* is a small phase, evidently at the northern fringe of distribution of the species, and thus shows what might be termed persistently juvenile features. As is well known, juvenile or impoverished extremes of the various species of *Plagiochila* can hardly be surely separated. Therefore the apparent intergradation may be a superficial, rather than fundamental, transition.

A remote similarity also exists between *P. floridana* and *P. diffusa*. The similarity in leaf-shape and insertion, the relatively short-decurrent postical, and moderately decurrent dorsal leaf-bases, and the similarity in cell-size and in the rather large, occasionally bulging trigones suggest that the two are related. Quite striking is the tendency (noted in the type specimens of both species) for the elongate marginal leaf-cells, especially just below the subapical spinose teeth, to be thick-walled parallel to the leaf-margins, thus forming a more or less discrete border, differing from the interior walls. This is more strongly marked in *P. diffusa* than in *floridana*, as far as has been observed.

In spite of these similarities, *P. floridana* differs in several respects from *P. diffusa*, particularly as follows: the leaves (at least above the shoot-middle) spread at an angle of only 40-45° (usually 50-60, occasionally 65-70° in *P. diffusa*), resulting in a very different facies; the underleaves, though minute, are usually discrete (vestigial in *diffusa*); the plants are less robust, 1.5-2.0, rarely 2.5 to 4.2 mm wide (mostly 4-5 mm wide in *diffusa*); the marginal teeth are less strongly developed, on an average, and usually less than 6-7 cells long x 3-4 (5) cells wide at base, terminated by a uniseriate row of 2-3, rarely 4 cells (in *P. diffusa* with the larger teeth 4-8 (9) cells wide at base x 8-12 cells long, terminated by a uniseriate row of often 4-6, occasionally 6-8 cells). Usually the different angles at which the leaves spread at once serve to separate the two species. Furthermore, *P. floridana* (and the allied *P. dubia*) always have leaves that are slightly to distinctly imbricate, in the moist condition; *i.e.*, the plants are able to form only a mod. *densifolia*. By contrast, all phases of *P. diffusa* seen, including the types of *P. diffusa* and *P. smallii*, are lax-leaved, with the leaves remote when moist; *i.e.*, the species appears to be unable to form anything but the mod. *laxifolia*.

The difficulty in separating the *P. floridana-dubia* complex and *P. diffusa* is demonstrated by the material from Mt. Olive, Miss. (*Schuster* 19167*a*; among *Trichomanis petersii* with *Lejeunea flava, L. minutiloba*). These plants, not very well-developed in most cases, are up to 3.2 mm wide. The leaves spread at an angle of 50-55° with the stem, except on the upper portions of shoots, where the angle may be merely 45°. Much of the material is impoverished, and the leaves then are distinctly less than twice as long as wide,

although mature leaves show the narrowly lingulate form typical of the *P. floridana* complex. A few plants show small propagula of the postical leaf-surface. The cells have very well-developed, mostly bulging, large trigones. The plants of this collection, when first examined, could scarcely be safely referred to *P. floridana.* However, the acute or subacute angle formed by the leaves and stem, on the upper portions of shoots, and the approximate to imbricate leaves, as well as the smaller maximum size (to 3.2 mm wide) all suggest *P. floridana.* Furthermore, the very characteristic border found in *P. diffusa* was not indicated, although the cell-walls of some plants were somewhat evenly thick-walled throughout all of the leaf. The disposition of this material as *P. floridana* therefore appears warranted, considerably extending the range of the species northward to a new limited point.

A further collection, superficially difficult to place between *P. floridana-dubia* and *diffusa* is that of Schuster 22853a; on *Carya,* at Hillsborough State Park. The plants are few and mostly poorly developed, and then show virtually edentate leaves (the apex often, however, bidentate); the most robust plants are only 2.7 mm wide, but show the characteristic leaf-orientation of *P. floridana,* with the leaves at an angle of 45-55°with the stem. These plants also show slight, almost evenly thick-walled marginal cells, but no trace of the peculiar border of *P. diffusa.* The plants again bear scattered few-celled propagula of the leaf-surface — often of the antical leaf surface, and have imbricate leaves, characteristic of *P. floridana.* The antical position of the propagula in this species is also noted elsewhere. I have not seen propagula on the antical surface in any of our other species, except *P. dubia* and *P. ludoviciana.* This position of the propagula may therefore form a further differential characteristic of *P. floridana.* More numerous observations confirming this are, however, needed.

Plagiochila aspleniformis sp. n.
Fig. 56

Quasi similis *P. asplenioidi* et rotundo-subquadratis foliis similibus nonnullis formis *P. asplenioidis;* dissimilis in frequentis terminalibus ramis, in libera adcrescentia propagularum ex inferioribus faciebus foliorum; in parvis cellulis foliorum (generaliter minus quam 23-25 μ latitudine media); in micante structure; in sparse irregularique dentatione rotundo-subtruncatorum folio-apicum.

Plantae mediocres vel magna (cum foliis 3.6-5.5 mm latus), sicca fulgentes, dense caespitosa, flavo-viridis; caules parum furcatum vel simplice; folia caulina patentia, late ovata vel ovato-oblonga, subintegra, apice plus minus truncatis, fere plana, margine postice parum decurrente; amphigastria minuta vel subnulla; cellularum marginalis parietibus aequaliter incrassatis. Typus: Hillsborough River State Park, Hillsborough Co., Florida (*Schuster* 22869), in herb. auct.

In green to *yellowish-green mats* (on coral limestone, on soil, and on sand and at the bases of trees). Shoot system consisting of a prostrate series of primary shoots, and of aerial, simple, once-furcate, or rarely monopodially branched, weakly ascending to loosely decumbent leafy shoots; *branches often furcate and terminal;* leafy shoots robust, 3.6-5.5 mm wide (occasional gemmiparous shoots only 2.6-3.5 mm wide). Plants *strongly shining when dry, often a peculiar yellowish-green* (due to yellowish pigmentation of the cell-walls), and with yellowish-brown to brown stems. Stems *ca.* (225-275) 310-350 μ in diameter, of elongate cortical cells (*ca.* 12-14 μ wide x 46-85, occa-

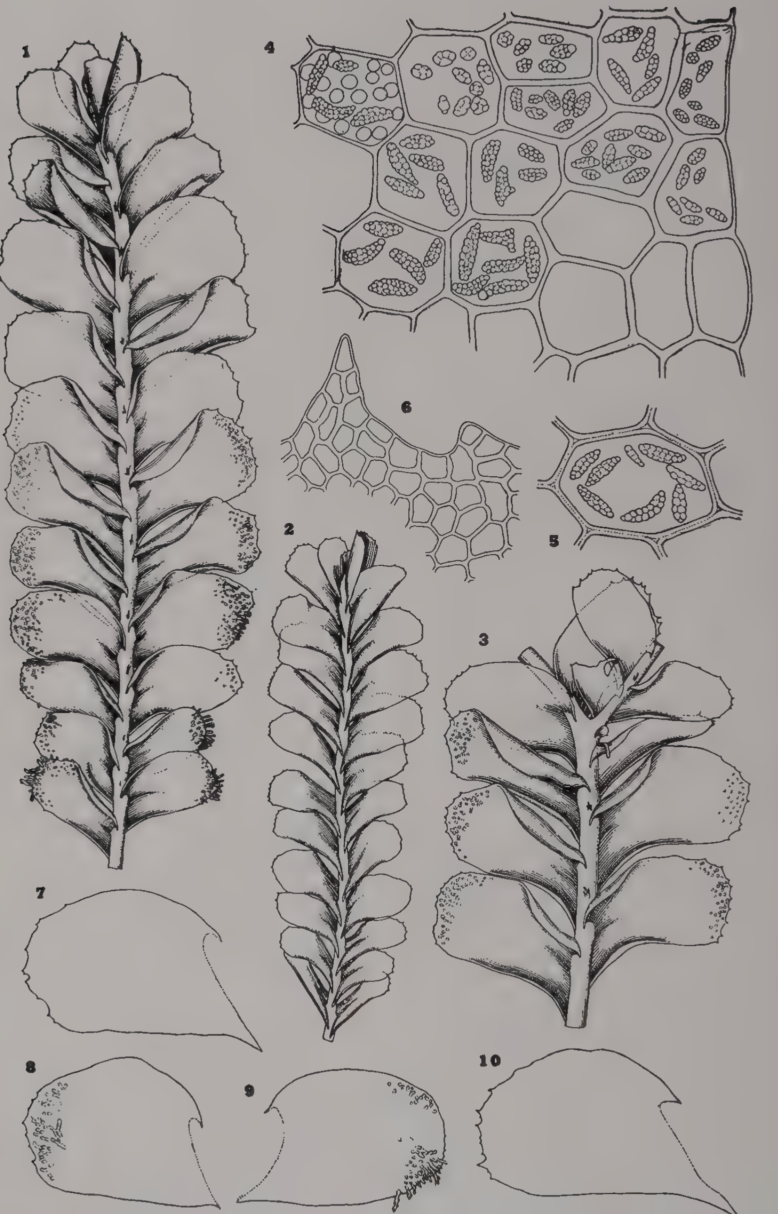

Fig. 56.—*Plagiochila aspleniformis* Schuster. 1. Mature shoot, with propagula, postical view (x 8.5); 2. Shoot, dorsal aspect (x 5.2); 3. Sector of very robust shoot, postical aspect, showing terminal branch at right, and propagula

sionally 90-100 μ long, strongly thick-walled, with walls often nearly as thick as lumen). Rhizoids absent on leafy aerial shoots. *Leaves contiguous to slightly imbricate, spreading laterally,* not postically secund (but usually *with antical and postical margins deflexed, thus with leaf postically concave*), at *ca.* a 65-75° angle with stem; leaves essentially broadly rounded-rectangular to ovate-rectangular, the *apices usually broadly truncate-rounded,* the *postical margin weakly or scarcely dilated above base,* lying nearly parallel to the antical margin (above the decurrent base), averaging 1700-1900 μ long x 1420-1800 μ wide to 1950-2050 μ long x 1500-1750 μ wide, at times narrower and more nearly ovate-rectangular, with apices broadly rounded rather than truncate (and then *ca.* 2100 μ long x 1670 μ wide), attaining a maximal length of *ca.* 2500 μ x 2000 μ wide; length varying from 1.05 to 1.38 × the maximal width; antical margin reflexed for most of its length, nearly straight above the moderately decurrent base, entire-margined; postical margin somewhat arched from the *short-decurrent base,* moderately or slightly dilated, *the margin only slightly arched* (and subparallel to antical) above the base, entire or subentire except sometimes on distal one-fourth; *leaf-apex typically subtruncate to rounded-truncate,* occasionally broadly rounded, *bearing usually* 5-10 *small, irregular, relatively inconspicuous, short but broad-based acute or subacute teeth* (1-2, occasionally 3-4 cells long, usually as wide as long); teeth formed of nearly isodiametric cells, the terminal cells 0.8-1.5 × as long as wide; postical leaf-margin short-decurrent (for up to one-fourth the merophyte length), the postical leaf-bases not closely approximated, *leaving much of the stem visible.* Cells in apical portion of leaf 19-23 x 20-25 (27) μ, in leaf-middle *21-25 μ wide* x 23-30 (33) μ long, in base 19-24 μ wide x 32-44 μ long (not forming a vitta); *cell-walls ± equally thickened, trigones essentially absent* (even under xeric conditions); marginal 2-3 rows of cells (and near postical base a border of 4-6 rows of elongate cells averaging 16-21 x 28-40 μ) *more strongly thick-walled, forming a weakly defined border;* oil-bodies rather *coarsely segmented,* mostly (3) 5-9 per cell, usually fusiform and ellipsoidal (then 3 x 9-13 μ to 3.5 x 6.9 μ, rarely 4 x 12 μ) to subspherical (then 4 μ to 3.5-4 x 4.6 μ); chloroplasts *ca.* 3-3.2 μ. Underleaves inconspicuous, small or minute, but nearly constant, formed of 2-several elongate cilia or ciliate laciniae. Asexual reproduction almost *constantly present, via propagula* produced on the distal fourths of the *postical* leaf surfaces. Habitually sterile.

Type.—Hillsborough R. State Park, Hillsborough Co., Florida (*Schuster* 22869).

Distribution.—Known only from Hillsborough R. in Hillsborough

(x 8.5); 4. Cells of leaf-margin, with oil-bodies and in upper left cell, chloroplasts (x 465); 5. Cell of leaf-middle, with oil-bodies (x 465); 6. Cells of leaf-apex, with two typical teeth (x 165); 7-10. Leaves, in 8-9, showing the restriction of propagula to distal one-third of the leaves (x 12.5). (Figs. all from *Schuster* 22864, Hillsborough R., Florida.)

State Park, Hillsborough Co., Florida (*Schuster* 22869, 22864, 22863; 33905a, with *P. floridana*) and from near border of Santa Fe. R., in O'Leno State Park, N. of High Springs, Columbia Co., Florida (*Schuster* 37276, 37276a). Both of the stations lie roughly within the so-called "Oligocene Island Area" of central and western Florida.

Ecology.—Frequent on loose, relatively dry, nearly pure sand of low banks or river terraces, there with *Lejeunea floridana, Mitchella repens,* etc.; occasionally also growing up to the fibrous root bases of *Sabal palmetto,* or over coral limestone (then with *Plagiochila ludoviciana, P. floridana, Lejeunea floridana,* etc.). Less often, on sandy banks, *Lejeunea cladogyna* is associated, the Partridge berry, *Mitchella repens,* undergoing ecesis in the *Plagiochila-Lejeunea* mats.

At the second known station for the species, the plants occur under strikingly similar conditions, on loose but damp sand, along low river terraces, again with *Lejeunea floridana!*

Differentiation.—This distinctive species appears to stand isolated among our nearctic species of *Plagiochila.* At first glance, it has the appearance of a disjunct variant or subspecies of the polymorphic *P. asplenioides,* forms of which it superficially resembles. This resemblance is emphasized by the large size (to 5.5 mm wide), the subsimple shoots, the rather distant to approximate ovate-rectangular to oblong leaves that are broadly rounded or rounded-truncate distally, the fine marginal teeth (which, as in *asplenioides,* are absent or vestigial on less robust plants), and the segmented oil-bodies.

However, the plants have several vegetative characteristics that set the species apart from *P. asplenioides,* among them (1) a peculiar yellowish-green, rather pellucid appearance of the leaves, contrasted to the eventually brownish stems; (2) the conspicuous shine of the dry plant (nearly or quite dull in *P. asplenioides*); (3) the leaves, even on the most robust plants, with the marginal teeth few, and mostly near the truncate apex of the leaf; (4) the leaves, even on very robust plants, with no tendency to be postically secund, but spreading laterally. Perhaps more important than the above characters as diagnostic features, are (5) the abundant production on the postical leaf-surface of leafy propagula; (6) the much smaller, non-collenchymatous evenly thick-walled leaf-cells; and (7) the ability to regularly produce terminal branches (Fig. 56:3). In these last characteristics this species differs from the species of the Sectio Asplenioides. The writer suggests that the similarities to this last section are due to superficial resemblances, and do not indicate a close phylogenetic connection. It should be noted, however, that under some conditions, *P. asplenioides* may produce leafy regenerations as described by Douin (1924). His figures are copied by Müller (1942, p. 125, Fig. 8h). In the writer's opinion, the ability, under certain conditions, to produce regenerations from the leaves does not imply that these are produced in nature, and therefore are not strictly comparable to the numerous propagula, freely produced in nature, that characterize *P. aspleniformis.*

In cases of doubt, the stem anatomy alone will separate *P. aspleniformis* from any phase of *P. asplenioides,* since the thick-walled, yel-

lowish cortical cells are narrow and bast-like, ranging from 12-15 μ wide x (45) 60-90 μ long (thus *ca.* 4-8 $\times$ as long as broad!).

In the absence of propagula, it is possible that (if the cell size is not determined) *P. aspleniformis* may be confused with edentate or paucidentate forms of *P. asplenioides*. However, a very considerable gap prevails between the known southernmost range of *P. asplenioides* (northern Georgia and South Carolina) and that of *P. aspleniformis* (ancient Oligocene Island of Florida). The writer suspects that *P. aspleniformis* represents part of the old tropical invasion, which survived in Florida only in the Oligocene Island region during the recent geological periods, and therefore is related most closely to tropical species. To date, no closely similar neotropical species has been found, in which reproduction by leafy propagula is known.

This species keys out near *P. virginica* and *floridana,* with which it shares similar cell-size, and the ability to develop propagula and terminal branches. Its relationships (though distant) appear to be with this complex. However, (1) the somewhat irregular teeth, small in size, and their restriction to the distal one-fourth of the leaf; (2) the equally thick-walled cells; (3) the very short, broadly rounded-oblong leaves all serve to separate *P. aspleniformis* from these two species. The nearly parallel-sided leaf might cause confusion with *P. diffusa,* a quite unrelated species, which also has the relatively small teeth of the leaves restricted normally to the distal one-fourth of the leaf. The exceedingly short-rectangular leaf-form, the slightly imbricate leaves, and the equally thick-walled leaf-cells serve as differential features from *P. diffusa.*

The leaf-cells of this species deserve emphasis. They appear to be virtually equally thick-walled, with at best small, concave, inconspicuous trigones. Under the most mesic conditions that were inhabited by the species (at the type stations), the median cells have relatively thin cell-walls, with minute or small concave trigones. Under the more "typical" conditions (*e. g.,* the site at which the species was most abundant), the plants occurred on loose dry sand some 8-12 feet above the river, on a river terrace — under distinctly xeric conditions. Here the plants had yellowish cell-walls that were evenly thickened (more strongly so in several marginal rows), except for the vestigial trigones which appear to be laid down first. Evidently, this species "behaves" somewhat like *Lophozia bicrenata,* a species unable to produce large trigones, but able to lay down equal layers of wall-thickening. Our other species of the complex lack the ability to develop thick-walled cells, although they may produce large trigones, which may become so large (as in xeromorphic forms of *P. virginica caroliniana*) that they are freely confluent. The behavior-pattern of the cells of this species, in the writer's opinion, is the single most important species criterion since this serves to set the species off from all other nearctic taxa.

The plants appear to be very freely propaguliferous under all conditions. In the few cases where the species was found with other Plagiochilae (*P. floridana, P. ludoviciana*) it was freely propaguliferous,

even though the associated Plagiochilae lacked propagula. Evidently a very slight stimulus is necessary to initiate propagula-formation in this species (even slighter — or at least qualitatively different — than in *P. ludoviciana*).

Sectio IX. HYPNOIDES Carl, emend. Schuster

Robust plants, ± green, dull, usually 3.8-5.5 mm wide, *laxly pseudodichotomously branched;* stems with cortex often brown, 2-3 (4) stratose. Leaves when dry postically secund, the shoots apically also often postically deflexed, especially *when dry, then subcircinate;* leaves notably *flat and laterally spreading when moist, densely imbricate (the ampliate postical bases shingled, hiding the stem)*, rather narrow (usually 1.5-2.2 × as long as wide), ovate-rectangulate to narrowly ovate-falcate, the postical base *distinctly ampliate, not convolute or modified to form a water-sac, ± cristate but notably short-decurrent;* postical margin, above base, *usually at nearly right angles with stem;* antical margin slightly concavely arched, reflexed, *long-decurrent;* leaves freely and usually *nearly uniformly spinose-dentate, from the decurrent postical base to the apex* (usually with 16-32 teeth), the antical margin entire, except for 1-2 preapical teeth. Cells strongly collenchymatous, moderate in size, usually 17-23 μ *wide in leaf-middle* and near base; basal cells little elongate, the *leaf not vittate;* oil-bodies usually 4-9 per cell, *distinctly segmented. Underleaves small to large,* usually *of a distinct* (sometimes bifid) *lamella,* armed or resolved into marginal cilia. *Asexual reproduction freely present, by propagula.*

Androecia intercalary, often basal on forks of a dichotomy — thus geminate.

The Sectio Hypnoides was delimited much more broadly by Carl than is done here. Carl (*loc. cit.*, p. 55-57) correctly emphasizes the dense-leaved, strongly distichous facies of the plants of this group. Carl admits that the group is probably closely allied to the Crispatae. He would separate the latter sectio from the Hypnoides on the basis of the more highly differentiated postical leaf-base, which is either cristate or involute. On this basis, *P. ludoviciana* would be referred to the Hypnoides, *P. miradorensis* to the Crispatae. Since these two species are closely allied in most respects, separating them into discrete species groups appears unnatural. A different basis, therefore, must be used in separating the Crispatae and Hypnoides, if this division into two sections is to be maintained. In the opinion of the author, the best grounds for such a division is on the basis of the degree of decurrence of the postical leaf-base. In the short-decurrent species (Sectio Hypnoides), there is no elaboration of a pronounced postical crista, or of a distinct water pocket. This is associated with a notably short decurrence of the ventral leaf-base (usually for *ca.* 0.2 the merophyte length!). Associated with this, the Hypnoides s. str. normally have sharply and nearly uniformly spinose-dentate to spinose-serrate leaves, the dentition being nearly uniform along the postical margin and extending in all cases down to the dilated basal portions of the

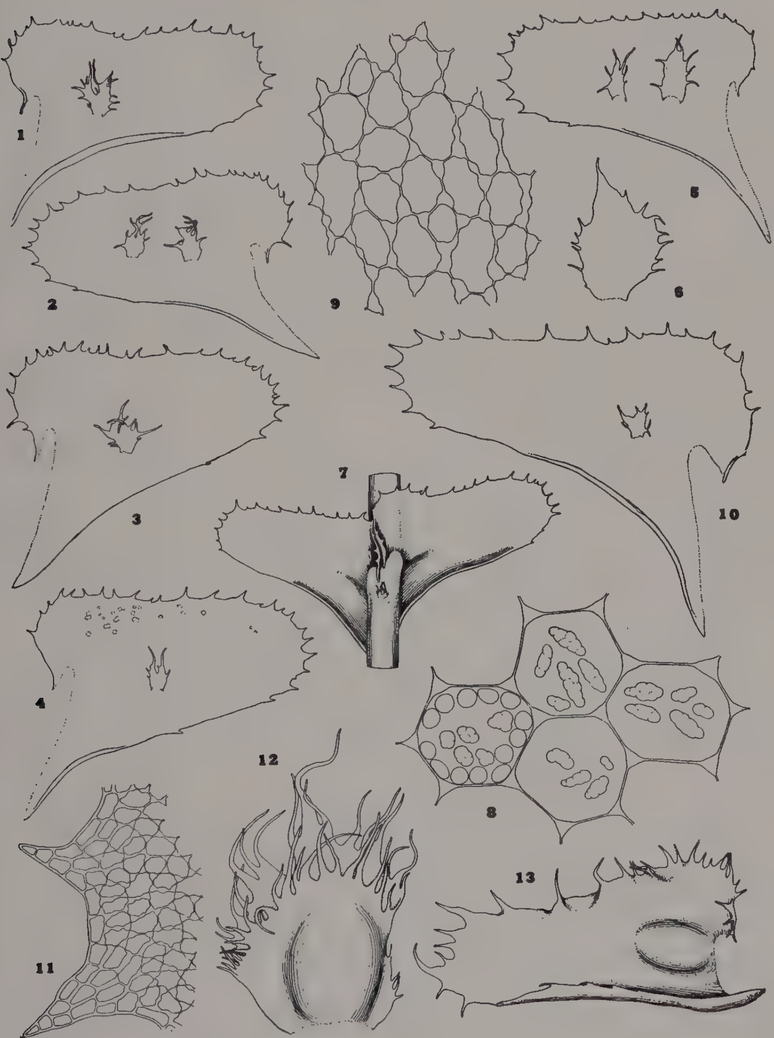

Fig. 57.—*Plagiochila hypnoides* Lindenb. 1-5. Leaves of the most typical and robust Floridian phase, with adjacent underleaves drawn to same scale (x 18); 6. Atypically large underleaf (x 18); 7. Shoot-sector in postical aspect, showing the juxtaposed and cristate postical leaf bases (x 15); 8. Median cells with oil-bodies (x 700); 9. Median cells (x 300); 10. Leaf and underleaf of mod. *megafolia* (x 18); 11. Cells of leaf-apex (x 135); 12. Juvenile perianth, lateral aspect, keel at right (x 24); 13. Female bract (x 18). (Figs. 1-6, 10, drawn to one scale; figs. 1-8, *Schuster* 33801c, Ross Hammock, Fla.; 9-10, Columbia, *Woronow*, ex herb. Th. Herzog; 11-13, *Schuster* 26018, Highlands Hammock, Florida.)

leaf and the decurrent basal strip, usually with undiminished vigor. In the Crispatae there is apparently always a more or less distinct differentiation between the distal and basal portions of the leaf, as regards degree of dentition; in some species (*e. g., P. ludoviciana* and its relatives) the teeth tend to be sharpest and most vigorous distally, with the basal part of the ventral margin entire or subentire; in others (*e.g., P. miradorensis*) the dentition is sometimes restricted to the leaf base, or at least this bears more highly elaborated teeth.

In contrast to the Hypnoides, the Sectio Crispatae (as delimited here) has a long-decurrent postical leaf-base, the decurrent strip running down for 0.5-0.75 the merophyte length, occasionally even 0.85-0.95. Associated with this, the dilated postical base is either sharply erect, standing stiffly away from the stem (forming a *crista*), or is even reflexed or convolute to a higher degree (forming a rudimentary type of *water sac*). No sharp division between these two types is feasible, as has been demonstrated by a careful study of the *P. ludoviciana-miradorensis* complex.

Except for the different degree of elaboration of the postical leaf-bases (and their decurrence), the Hypnoides and Crispatae are essentially identical. Both groups freely produce terminal branches, although ramification is always diffuse; both groups have a notably long-decurrent antical leaf-base; both "tend" to develop geminate androecia, *i.e.,* androecia sessile at the bases of apical bifurcations of leading leafy axes; and both groups regularly show the production of propagula. The distinction of the two sections is further treated under the discussion following the treatment of *P. hypnoides* (see p. 68).

Delimiting the Hypnoides as is done here, the group is represented by a single species in the United States, which has not before been reported from our area.

PLAGIOCHILA HYPNOIDES LINDENB.

Figs. 57-60; 61:6, 9; 62:4-5

Plagiochila hypnoides Lindenb., Spec. Hep. 644, 1844; Carl, Annal. Bryol. Suppl. Vol. II:57, fig. 7, f, 1, 1931.
Plagiochila affinis Gottsche, Mex. Leverm. 154, pl. 8, 1863?
Plagiochila sinuata Gottsche, Mex. Leverm. 151, pl. 9, 1863?

Plants *robust,* deep green to olive-green, nearly dull when dry, the aerial shoots mostly 2-5 cm high, subsimple to 1-2 × pseudodichotomous, erect to suberect, or spreading away from substrate, often somewhat arched or pendulous, (3.2) 4.0-5.5 mm wide. Stems rigid, (240) 260-320 (400) μ in diameter, rarely stouter, yellowish to yellowish-brown with age. Rhizoids few, virtually or quite absent on aerial shoots. Leaves *very densely imbricate,* laterally spreading when moist, postically connivent and secund when dry, *obliquely ovate to ovate-oblong,* (1050-1075) 1100-1175 μ wide at level of postical dilation x (1600-1775) 1900-2150 μ long in our forms (in robust plants to *ca.* 1400-1450 μ wide x 2250-2550 μ long); *length usually* 1.5-1.65 (1.85-2.0) × *the maximal width; leaves short-decurrent postically,* the base

above the *decurrent strip erect, dilated,* 1-*several spinose-dentate,* never forming a water-sac but sometimes narrowly reflexed; *postical base strongly arched and ampliate,* the ampliate bases shingled, with the inner margins erect, *resulting in two lines of vertical, closely juxtaposed spinose-dentate ridges, thus distinctly cristate;* entire postical margin and apex, with ± subequal, sharp, spinose teeth, *usually* (17) 21-26 (32) *teeth per leaf,* of which 1-3 are situated on the apical half of the antical margin; remainder of antical margin sharply reflexed, the *cnemis well developed, the antical base very long decurrent* (the line of leaf-insertion from (850) 950-1200, sometimes 1450 μ long); leaves, except for cristate basal portion, the occasionally sinuous postical margin and the reflexed antical margin, nearly plane; teeth of leaves mostly 3-5 (7-11) cells long, 2-4 cells broad at base, the *apices commonly uniseriate for* 2-3 (4-6) *cells,* the cells usually 20-25 (30) μ x (11) 13-17 μ wide at base. Cells *strongly collenchymatous, trigones large to subconfluent,* the marginal cells often slightly elongated and more thick-walled (otherwise leaves not bordered); subapical and median cells subequal in size, (15-17) 18-21 (23) μ wide x (20) 23-27 (medially often to 32-34) μ long; basal cells near midline of leaf (17) 20-23 (27) x (25) 28-36 (42) μ long; cells near postical leaf-base, along margins, often rectangulate and elongated, 24-35 x 14-16 μ, ± equally thick-walled. Oil-bodies largely 4-6 (8-9) *per cell,* rather *coarsely segmented,* ovoid to ellipsoidal and from 2.5 x 5 to 3-3.5 x 9-10 (rarely 11) μ, occasionally spherical or subspherical and then 4 μ to 4 x 5 μ, to 4-4.5 x 7.5-11 μ, a few to 5 x 7-7.5 μ, composed of *few and coarse, protruding segments;* chloroplasts averaging 4 μ, averaging smaller than oil-bodies. *Underleaves usually distinct throughout,* but often so small as to be seen with difficulty, commonly hidden under the dilated, ampliate leaf-bases, varying usually from 330-450 μ long x 200-350 μ wide (including cilia), but *occasionally very large* in isolated instances, then to 600 μ wide x 1050 μ long or even 750 μ wide x 1350 μ long, the underleaves usually bilobed and variously ciliate, the largest ovate to lanceolate, ciliate on margins. Asexual reproduction via *propagula formed from the postical leaf-surfaces,* usually present in abundance; leaves uniformly persistent.

Dioecious; in our area usually sterile, but occasionally with juvenile perianths. Perichaetial bracts *ca.* 2200-2300 μ long x 1225-1300 μ wide, narrowly oblong-ovate, the postical base rather weakly dilated, the oblong distal half subtruncately terminated; margins with *ca.* 30-36 spinose, strongly variable teeth, the postical base with the teeth often rather crowded, although smaller; base of bracts concave, sheathing perianth-base, the postical margin more or less strongly crispate-undulate. Perianth (juvenile) to 1600 μ long, with cilia, the body then *ca.* 1000 μ long, sharply keeled dorsally (the keel commonly winged and often 1-4-spinose-dentate), inflated basally, complanate apically; mouth oblique, the antical keel longer than the postical, the *mouth longly and rather densely ciliate-laciniate,* the longer cilia 3-4 cells wide at base x 16-24 cells long, a few to 8 cells wide x 32 cells long, tortuous, the apex uniseriate for a length of commonly 9-14

cells. Androecia short, often of only 3-4 (5-6) pairs of bracts, compact, the bracts closely imbricate; androecia commonly situated at bases of terminal forks of leading axes, then *geminate, with vegetative proliferation distally.*

Type.—Brazil (*Willd.*)

Distribution.—A very widespread and polymorphic neotropical species, ranging northward from BRAZIL: S. Paulo, Alto da Serra, leg. F. C. Hoehne, 1920, No. 142, det. Th. Herzog!; Pariti, R. Purno, upper Amazon (Trail, 1874; close to *P. serrata*!); Rio Negro (Spruce Hep. Spruceanae, Amaz. et And. No. 492, as *P. hypnoides* var.), differing in the more copiously ciliate-dentate postical leaf-base, in which it approaches both *P. serrata* and *P. falcato-serrata.* Of two other specimens (NYBG) in the Hep. Spruceanae, Amaz. et And. without number, from "Pará, et fl. Aripecurú" distributed as *P. serrata,* one appears to be typical *P. hypnoides,* the other represents *P. serrata.* PERU: Rio Hualaga, Dept. Soreto (leg. *Killip* 27857, det. Th. Herzog!); COLOMBIA: Florencia, Cagneta (leg. Woronow *No. 59,* det. Th. Herzog!); BOLIVIA: Hac Simaco bei Tipuano, 1400 m. (leg. G. Buchtian, 1920, *No.* 110!; postical leaf-bases long-decurrent, with perianths and propagula; either identical or very close to *P. ludoviciana;* underleaves minute or absent). COSTA RICA: Parismina (*leg. M. Valerio No.* 68!, July 1928; det. et leg. Th. Herzog, 1954); Hamburg Finca, Prov. Lemon (*Standley* 48685, det. Th. Herzog!); Boxuca, "ad Pacific" (*Tonduz* 15663!; extremely large and delicate phase with subentire leaves); COSTA RICA, det. Stephani! SURINAM (*Miquel!*); FRENCH GUIANA: Grant's Rd., Metabon (*Broadway* 888; unusual form with subentire leaves); TRINIDAD (No loc. data, Fendler, 1878-1880!); Blanchisseuse Rd., near St. Patrick Estate (Broadway 7899; phase with small underleaves). JAMAICA (*Wolle!*). PANAMA: prope Villam Crucis, January 1847 (herb. Hooker, NYBG; typical but with rather small underleaves). CUBA: La Prenda, Oriente (leg. *Hioram and Maurel* 2601, 4120!); Sierra de las Yeguas, San Diego de los Baños (*Leon* 5238); Wright, *in* Hep. Cubensis Wrightianae!. PUERTO RICO: Laguna San José, Rio Pedras (*F. M. Pagan* 418!, male); Aibonito (*Pagan* 577! mixed with *P. dubia;* as *"P. ludoviciana"* det. Pagan, Y); Rocky Hill near Pueblito del Rio (*Britton* 9423!; a small mod. *subintegrifolia,* det. as *"P. ludoviciana"* by Evans, Y); Island of Vieques (*Pagan, del Valle and Garcia* 104!); Utado *Pagan* 2170; form with small underleaves!). ST. THOMAS: (*Britton and Marble* 1453); ST. JAN (*Bethania, Britton and Shafer* 360!); and the BAHAMAS: New Providence (*Britton* 253, 3221, 6555; *Brace* 3, 4, 6). The plants from the Bahamas and from the Virgin Islands have been reported as *P. ludoviciana* by Evans (1911, 1918).

Also reported by Gottsche from MEXICO (Jalapa). *P. sinuata* Gottsche, from Zacuapan, Dept. Vera Cruz, Mexico, is, in the author's opinion, probably identical; it differs, according to Gottsche, in the absence of underleaves and the differently shaped leaves. The Mexican *P. affinis* Lindenb. and Gottsche, as figured in Gottsche (1863), also appears to be very closely allied, also lacking underleaves. However, Carl (1931), studying a series of specimens from Costa Rica (leg. Stanley) admits that the degree of development of the underleaves is subject to considerable variation in this complex. As in *P. ludoviciana,* weak forms may lack underleaves almost entirely, while strong individuals may possess them. As a consequence, the degree of development of underleaves (remnants are always to be found!) — or the degree of suppression, cannot, by itself, stand as a species criterion in this complex. Indeed, the material from Colombia (*Woronow* 59, det. Th. Herzog, as *P. hypnoides*)

virtually lacks underleaves on some plants, while in others they are so small that they are easily overlooked.

The plant occurs northward to southern FLORIDA: Ross Hammock, N. of Homestead, Dade Co. (*Schuster* 33801c p.p.); Paradise Key, Everglades Ntl. Park, Dade Co. (*Schuster* 20182a, p.p.; 20150, 20182, 20182a, p.p. with *Radula australis;* 19907, 20180, 20158, 22891, c. androecia; 22606, 20156, 20154; *Small and Lowe* 7029, juvenile!); hammock forest, section 12 of Long Key Pineland, Everglades Ntl. Park, Dade Co. (*Schuster* 22095); deep hammock forest, at E. end of Long Pine Key, Dade Co. (*Schuster* 36827b, 36832; 36832b, with *Lejeunea laetevirens, Rectolejeunea brittoniae;* 36827, with *Rectolejeunea phyllobola;* 36827a, with *Mastigolejeunea auriculata*); deep Mahogany Hammock, 2.5-3 mi. W. of "SW. bend of Ingraham Hwy." just SW. of end of Long Pine Key, Everglades of W. Dade Co. (*Schuster* 37301e, 37326b, 37323d, 37308a, 37308d; 37308g, with *Neckera disticha;* 37369b, 37336b, 38328c, 37321,, 37368a, 37368, 37341, 37366b, 37342c, 37355d, 37366a, 37358a, 37357, 37366, 37352a); Royal Palm Hammock, Collier-Seminole State Park, Collier Co. (*Schuster* 26130, 20420, 20415, 20412a, 20282, 20421, 20295a, 20270a, 26132b); Highlands Hammock State Park, 6 mi. W. of Sebring, Highlands Co. (*Schuster* 19942, 26018, c. per juv.; 19954d, 20111, 20092, 26015, 26016, 26014a, 26024a); Mathesson Hammock, Old Cutler Rd., Dade Co. (*Schuster* 22688, 22681, 22690); Timm's Hammock, N. of Homestead on Bauer Drive, Dade Co. (*Schuster* 22851, 22857b); Costello Hammock, near Silver Palm, Dade Co. (*Schuster* 22964b); Freeman Hammock, Arch Creek Prairie, Dade Co. (*Small, Mosier and Small* 6145!); in Everglades near Camp Longview (*Small and Wilson* 1545*a*!; male); Hammocks near the Homestead Trail, near Camp Longview (*Small and Wilson* 2051, 2059!); near Homestead Road, between Cutler and Longview Camp (*Small and Carter* 1370 p.p.!); Elliott's Key, Monroe Co. (*Small and Nash* 468!; form with unusually small underleaves); Timm's Hammock, Dade Co. (*Small and Mosier* 5290a; *Small, Mosier and Small* 6981!); Nixon-Lewis Hammock, Dade Co. (*Small and Mosier* 5246 p.p.!); *Paurotis* Hammock, on Cape Sable, Monroe Co. (W. S. Phillips herb. *No.* 115); Deep Lake, Collier Co., on *Acer rubrum* (W. S. Phillips herb. *No.* 46!). In addition, two collections of somewhat juvenile plants appear to belong here: Palma Vista Hammock, near Paradise Key, Dade Co. (*Schuster* 22148); Brogdon Hammock, Dade Co. (*Small and Mosier* 6232; determined, with question, as *P. floridana* by Evans); Redlands Hammock, Kings Hwy., NW. of Homestead, Dade Co. (*Schuster* 42129a, 42119a).

Very rarely occurring northward to central Florida, where apparently localized in the eastern edge of the Oligocene Island region: near Oviedo (*Rapp* 85!, p. min. p., among *P. floridana,* Y); on rotten logs, 10 mi. S. of Sanford, Seminole Co. (*W. L. Dix,* March 1950!; det. by Evans as "*P. ludoviciana,*" in herb. Y; the plants are a typical, if rather small, phase and bear androecia; the androecia in part geminate and fasciculate, with innovations from just below or even within the androecium that are immediately androecial); Big Tree County Park, 3 mi. N. of Fern Park, Seminole Co. (*Schuster* 42178, 42179a).

Except for the isolated collections from Highlands and Seminole Counties the species appears restricted to the Everglades of southern Florida. It was previously unknown from the United States, although numerous previous collections had been made, almost all misdetermined for *P. ludoviciana.*

Ecology.—A widespread species, usually at the bases of trees or on fallen lianas or logs, usually in deep evergreen forests; also fre-

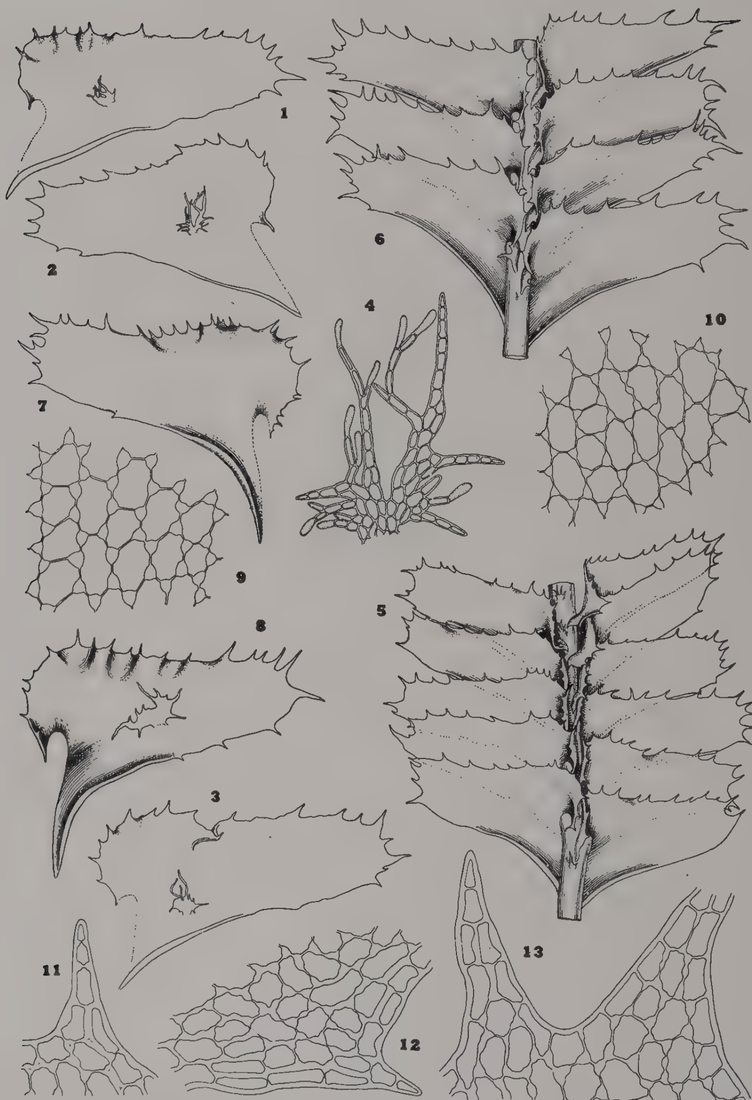

Fig. 58.—*Plagiochila hypnoides* Lindenb. 1-3. Leaves and underleaves (x 16); 4. Underleaf from fig. 2 (x 80); 5. Shoot-sector of robust phase, postical aspect (x 11); 6. Shoot-sector of phase with largely vestigial underleaves (x 17); 7-8. Two leaves and underleaf (x 13); 9. Basal cells (x 190); 10. Median cells (x 190); 11. Tooth of postical margin (x 190); 12. Tooth near base of postical margin (x 190); 13. Cells at leaf-apex (x 190). (Figs. 1-5, *Schuster* 20182, Paradise Key, Fla.; 6-13, *Schuster* 19954d, Highlands Hammock, Fla.)

quently forming festoons on twigs and small branches. The local plants at the bases of tree trunks, associated with various Lejeuneae (*Lejeunea longifissa, L. minutiloba, L. glaucescens, Ceratolejeunea laete-fusca, Cololejeunea diaphana* and *contractiloba*), *Radula australis,* and such mosses as *Neckera disticha.*

Perhaps more common high on tree trunks of a variety of trees. For instance, on *Quercus virginiana,* together with *Ceratolejeunea laete-fusca, Cheilolejeunea rigidula, Mastigolejeunea auriculata* (*Schuster* 19954d), or on bark of *Persea borbonia,* with *Frullania squarrosa, Mastigolejeunea auriculata* (*Schuster* 26132b), on bark of *Exothea paniculata* (with *Radula australis, Cheilolejeunea clausa, C. rigidula, Lejeunea laetevirens* and *bullata, Mastigolejeunea auriculata*) and also on bark of *Citharexylum fruticosum, Carya* sp., and *Laurocerasus.* In addition to the preceding hepatics, there are also associated *Lopholejeunea subfusca,* rarely *Frullania riojaneirensis,* and a series of other Hepaticae (*Cheilolejeunea clausa, Ceratolejeunea cubensis, Lejeunea glaucescens, Cheilolejeunea decidua, Taxilejeunea* sp.) and mosses (*Neckera undulata*). The species also occasionally occurs at tree-bases (as on *Elaphrium simaruba*), with *Radula australis, Lejeunea laetevirens,* etc., forming the matrix in which the fern *Campyloneurum phyllitidis* undergoes ecesis.

In the southern tip of Florida occasionally, in dense hammocks, forming weak festoons on twigs and small branches; then often with *Radula australis,* or with *Caudalejeunea lehmanniana.*

Variation and Differentiation.—A polymorphic taxon, to which will probably be referred, on careful study of the neotropical representatives of the group, a whole series of recently proposed "species." Reference has already been made to the fact that, particularly with variation in robustness, there is considerable variation in the size of the underleaves; in extreme cases they may be almost obsolete. The regional collection, (*Schuster* 33801c), is "typical" in that the underleaves are rather large and easily observed, *if* the ampliate leaf-bases are pushed away from the stem (Fig. 59:4-5); by contrast, the rather robust and well-developed plants of *Schuster* 19954d, in some cases (Fig. 58:6) may show virtually underleaf-free stems, while other stems of the same collection may possess rather large and obvious underleaves (Fig. 58:8); the great disparity in degree of development of underleaves within the same small patch of plants suggests this character has been much overemphasized as a systematic criterion.

If the degree of variation in leaf-shape and in dentition in the allied *P. ludoviciana* may serve as a criterion, we can expect to find a wide range in degree of development (or suppression) of dentition in this species. Some of the extremes have surely been described as different species. Carl (1931, p. 57) also entertains this opinion, stating: "Vielleicht müssen noch andere Arten zu *P. hypnoides* gestellt werden, wenn die Variationsbreite dieser offenbar vielgestaltigen Art Berücksichtigung findet." The variation in leaf-shape of this species appears to be somewhat different from that occurring in

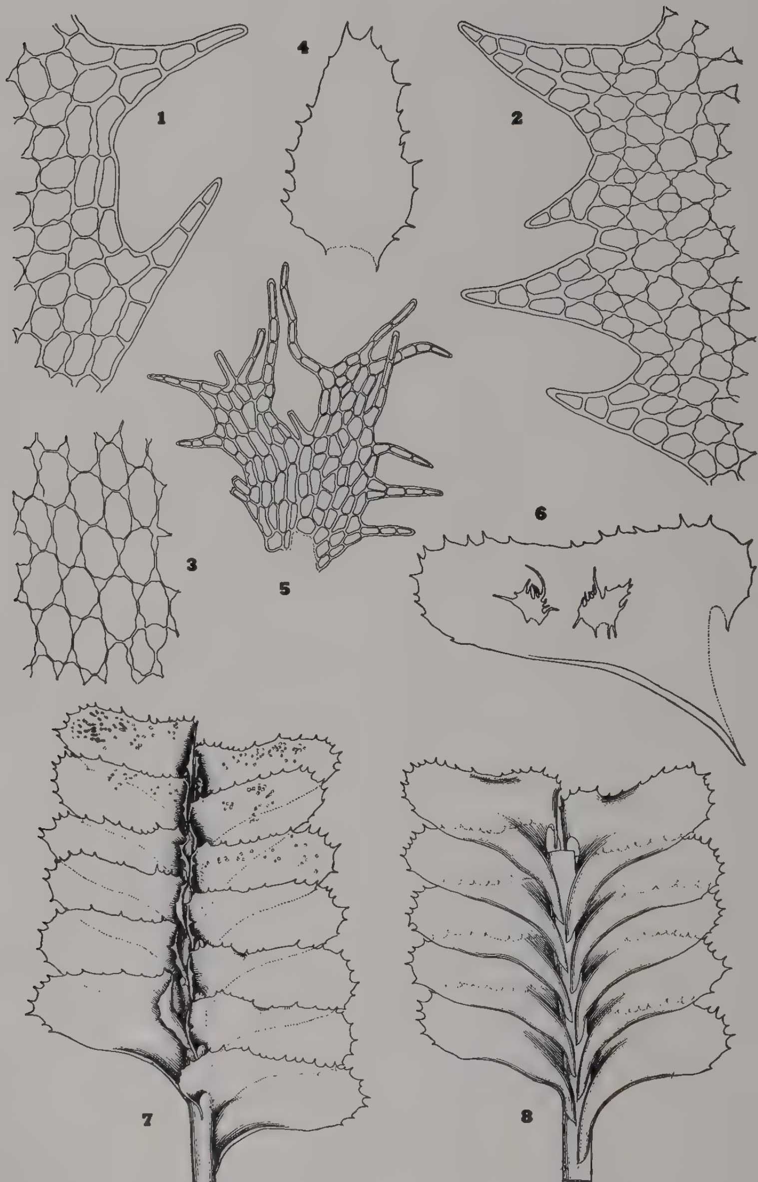

Fig. 59.—*Plagiochila hypnoides* Lindenb. 1. Cells from postical leaf-base above decurrent portion, showing typical dentition (x 240); 2. Cells of leaf-apex (x 240); 3. Median cells (x 240); 4. Extremely large, atypical underleaf (x 21.5); 5. Normal underleaf (x 115); 6. Leaf and, to same scale, two under-

the closely allied *P. ludoviciana.* The leaves are always narrow and elongate, with the length from a minimum of 1.4 to a maximum of 1.9, rarely 2.0 × the width at the widest point of the ampliate base. They always possess at least 1-2 spinose teeth just above the short-decurrent postical strip, and most often bear 1-several spinose teeth even on the decurrent strip. The teeth are always well developed, at least in our phases, and usually show little or no differentiation between the subapical and apical as regards size. However, occasionally (*Schuster* 19954d; Fig. 58:6-8) the teeth are notably coarser, and the apical may be sharply spinose, the leaf-apices becoming more nearly lacerate-laciniate.

With our present knowledge, *P. hypnoides* is restricted to plants with three critical features that, taken as a whole, serve to separate it from other regional Plagiochilae: (a) the leaf-margins, from the commonly narrowly subtruncate apex to the ampliate and decurrent postical base, are sharply and rather regularly spinose-dentate; (b) the distinctly ampliate and spinose-dentate postical base is short-decurrent, with formation of a vestigial crista — and never of a water-sac; (c) ciliate-dentate underleaves, even if vestigial ones, are present.

In the short-decurrent postical leaf-bases which are never broadly reflexed, *P. hypnoides* is, at least in theory, sharply separable from the otherwise very similar *P. ludoviciana.* In actual practice, this distinction is often difficult to maintain. However, it seems evident that the difficult transitional forms probably all represent weakly developed phases of *P. ludoviciana.* As a consequence, it must constantly be kept in mind that all short-decurrent, spinose-dentate, dense-leaved Plagiochilae occurring in the southeast cannot automatically be referred to *P. hypnoides.* In most respects, these two species are extraordinarily similar. Indeed, in antical aspect, the two are often nearly inseparable. Both species abundantly produce slender leafy propagula from the postical leaf faces, and both have leaf-cells and segmented oil-bodies with essentially identical dimensions. In both *P. hypnoides* and *P. ludoviciana* there is a similar response in the living plant to drying: the leaves become ± strongly postically secund and connivent, and the shoot becomes postically arched and curved, although hardly circinate. As a consequence, dry plants commonly appear very narrow, and quite linear, in antical profile.

The regional plants, as is so common with our other Plagiochilae of tropical derivation, are somewhat smaller than the material from the tropics which I have had occasion to study. They are mostly 3-3.5 mm wide, less often (*Schuster* 19954d, 20092, 20182) to 4.4-5.0 mm wide; well-developed plants from the tropics may be 5.0-5.5 mm wide or more. Except for this, they match almost perfectly, in all respects, such plants of *P. hypnoides* as those from Costa Rica (*Standley* 48685) and from Colombia (*Woronow* 59). One characteristic, in particular, equally developed in all collections of *P. hypnoides* seen,

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leaves (x 21.5); 7. Shoot-sector, with propagula, postical aspect (x 12.5); 8. Shoot-sector, antical aspect (x 12.5). (All from *Schuster* 33801c, Ross Hammock, Fla.)

deserves emphasis. Although the postical leaf-base is short-decurrent, the postical, ampliate base is somewhat reflexed-circinate due to its curved line of insertion, forming a postically open, in extreme cases ± conical basal pocket, although not a water-sac or crista in the strict sense.

Almost all of the regional plants studied were sterile, but bore an abundance of filiform, slender propagula. In two collections (*Schuster* 26018, 20092) immature perianths were developed. The female bracts seen were more oblong and narrower than those commonly found in *P. ludoviciana* (compare Figs. 57:13 and 61:3). They also were more sharply spinose-dentate or even laciniate-dentate, with the postical bases freely dentiferous. With study of a series of gynoecia, these differences largely disappear. In *P. ludoviciana,* the most spinose-leaved and attenuate-leaved forms (Fig. 64) have bracts that are as narrow and elongate, and are almost equally copiously dentate basally (Fig. 64:2-3). The immature perianths showed a great similarity to those of *P. ludoviciana.* The antical keel was similarly elongated, and was either in the form of a vestigial narrow lamella or was broader and bore 1-several small teeth near the base (Fig. 57:12). The postical keel was similarly abbreviated, with the consequence that the mouth was distinctly oblique. The very great degree of variation in development of the cilia in *P. ludoviciana* is clear from the figures (Figs. 61:2; 64:7; 62:2; 65:3-4); it probably will be found to include that of *P. hypnoides.* However, the few perianths of *P. hypnoides* seen (Fig. 57:12) differ in one respect: the cilia are longer and more tortuous. Several collections (*e.g., Schuster* 22891) have also been seen with androecia. These are short, often of only 3-4 pairs of bracts, compact, and often situated at the bases of furcate branches (thus geminate); they always proliferate vegetatively distally.

Juvenile forms of *P. hypnoides,* in which the aerial stems are short and simple, are frequent in our area. These may be virtually impossible to recognize, since they often do not show the marked shingling of the leaves characteristic of mature plants. Such plants may be confused with members of the Contiguae. However, prolonged search will generally reveal at least a few lamellate underleaves (Fig. 60:2, 4) that are suggestive of those of more "normal" *P. hypnoides.*

To our south, *P. hypnoides* becomes a more problematical taxon than within the immediate region here treated, since a number of very closely allied species inhabit the neotropics. The most immediately allied are, perhaps, *P. serrata* (Roth) G. L. et N., and *P. falcato-serrata* Carl ex Herzog. Both of these species have the postical leaf-bases more sharply and conspicuously ciliate-dentate, and *P. falcato-serrata,* in addition, has a basally more conspicuously ampliate leaf. From the restricted material of *P. serrata* available, it seems possible that *P. hypnoides* and *P. serrata* represent the extremes of a single variable taxon. However, no plants showing a clear-cut approach to *P. serrata* have been seen from our region.

P. serrata, in some respects, serves to connect the Hypnoides with the Crispatae. In at least the robust extremes of this species (*e.g., Richards* 827, British Guiana, near Akaio Landing, Cuyuni R.) the decurrence of the leaves ranges up to about 0.35-0.4 the merophyte length. However, in the Brazilian plants distributed by Spruce (Hep. Amaz. et And.: Para et fl. Aripecuru) the decurrence is perhaps only 0.25-0.3 the merophyte length. In both of these collections the leaves

are more narrow and drawn out than in the more ovate-triangular leaved *P. hypnoides,* and the dilation of the postical base is considerably less marked. As a consequence, the stem, in postical aspect, is not totally obscured by the leaves. Whether these differences are constant remains to be established. In any case, the more sharply spinose-dentate postical base will, in general, serve to separate *P. serrata* from

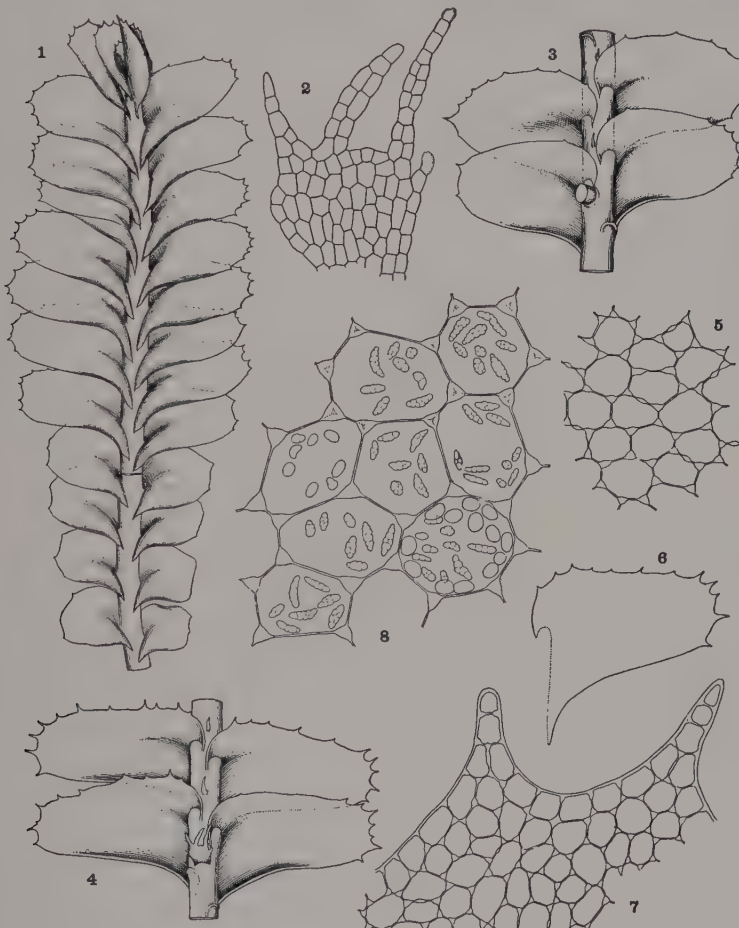

Fig. 60.—*Plagiochila hypnoides* Lindenb., juvenile extreme, with superficial "intergradation" to *P. virginica.* 1. Shoot, antical aspect (x 13.5); 2. Large underleaf (x 100); 3. Juvenile shoot-sector, postical aspect (x 18); 4. Shoot-sector, more nearly mature, postical aspect (x 16 5); 5. Median cells (x 190); 6. Leaf (x 18); 7. Apical cells (x 190). *Plagiochila virginica* Evs. 8. Median cells, with oil-bodies and in lower right, chloroplasts (x 460). (Figs. 1-7 from plants collected at Brogdon Hammock, Fla., *Small;* 8. Unicoi Gap, Georgia, *Schuster;* see in Fig. 44.)

P. hypnoides, although the number of teeth varies. For example, there are only 2-3 subbasal teeth in the aforementioned Brazilian plants of *P. serrata;* these, however, are much sharper and more prominent than in *P. hypnoides.* In the Brazilian plants the leaves are also more strongly falcate and curved, with a more concavely arcuate antical margin than in *P. hypnoides.* The British Guiana plants cited above do not show as distinctly falcate a leaf-form, however, although the leaves remain nearly as narrow as in the Brazilian plants.

The plants of *P. thysanotis* Spruce (as typified by the Hep. Amaz. et And., from the Rio Negro) are also very significant in fixing the limits between Hypnoides and Crispatae. These plants have the strongly narrowed and falcate leaves of the Brazilian plants referred by Spruce to *P. serrata;* they have similarly, but more strongly spinose margins; particularly the postical base is strongly spinose-ciliate with about 4-5 curved and often reflexed, tapering ciliform teeth occurring on the margin of the postical decurrent strip. These plants, furthermore, have the decurrence relatively strongly developed, the crispate and cristate, spinose-ciliate postical strip being decurrent for at least 0.5 the merophyte length on mature leaves. Stephani (1905, p. 507) places *P. thysanotis* in synonymy under *P. serrata;* the plant may be a robust, maximally dentate phase of this species. However, the more decurrent postical base suggests that two species may be at hand. The lack of other than vestigial underleaves in *P. thysanotis,* even on mature shoots, is a notable feature of the species.

The preceding study of *P. hypnoides* and its relatives suggests that, together with *P. falcato-serrata,* a difficult complex is at hand whose comprehension will require much more work. The four related taxa may be tentatively separated by the following key:

1. Leaves narrowly ovate-triangular, not strongly falcate, the postical base rather strongly dilated, with (0) 1-3 relatively small teeth; underleaves, at least on robust and mature shoots, discrete and often very large, dentate but not longly ciliate. .... *P. hypnoides*
1. Leaves lingulate-triangular to lingulate-falcate. 2
   2. Leaves with postical base not strongly ampliate, the straight postical margin simply rounded gradually into the postical decurrent strip; postical base sparingly dentate to ciliate-dentate, with only 3-5 teeth of decurrent strip. 3
      3. Underleaves distinct; postical base only 0.25-0.35 (0.4) decurrent, the decurrent strip with 2-3 spinose but relatively small teeth. .... *P. serrata*
      3. Underleaves vestigial; postical base *ca.* 0.5 decurrent, the very conspicuous, crispate and cristate decurrent strip armed with 3-4 (5) long and curved, spinose-ciliate teeth. .... *P. thysanotis*
   2. Leaves with postical base very markedly ampliate, strongly arched; postical decurrent strip curved, closely toothed with spinose teeth; underleaves large, lamellate, densely ciliate. .... *P. falcato-serrata*

A study of the preceding species, and of the closely allied *P. cristata,* suggests that these species, all indubitably belonging to the Hypnoides, are separable from the Crispatae chiefly on the basis of the tendency for sharp dentition of the postical leaf-bases, coupled with

a tendency for the decurrence to be markedly shorter. In none of these species does the decurrence ever appear to exceed 0.5 the merophyte length; in the Crispatae it rarely is as low as 0.5 the merophyte length, and the postical base is either edentate or virtually so or else provided with only 2-3 very small teeth (*e.g.*, in *P. miradorensis*). There is another associated tendency in the Hypnoides, which holds for all but exceptional species such as *P. blepharobasis*: the leaf-margins "tend" to be rather uniformly serrate to spinose-dentate from the base to the apex. Only in *P. blepharobasis* is the dentition reduced distally, with the Hypnoides-like dentition confined to the short-decurrent base (see Herzog, 1932, Fig. 9a-b). Finally, in the Hypnoides we find a marked tendency for the underleaves to be lamellate, the base being formed by a marked, sometimes 2-4-lobed and crispate lamella, the margins more or less ciliate. Such underleaves are typical of *P. hypnoides, P. falcato-serrata, P. blepharostoma, P. serrata,* etc. It is only very rarely that the underleaves are strongly reduced (*i.a.*, in *P. thysanotis* and *P. hoehni* Herzog — see Herzog, 1932, p. 220, Fig. 11g-i). By contrast, the Crispatae normally possess underleaves that are divided into narrow laciniae or cilia, either virtually to the base or to within one-fourth of it; they also often show marked reduction of the underleaves, and such typical members as *P. perbella* Herz. (Herzog, 1952, p. 77, Figs. 10-11) are described as with the underleaves "omnino nulla," although vestigial underleaves surely must occur.

Section X. CRISPATAE Carl

Plants *relatively robust,* 2.5-4.5 (5.5) mm wide x 2-8 cm long, spreading from substrate and often pendulous or forming festoons, light green to olive-green or olive-brown, the stems often brown, *dull* or nearly so. Branching of weak plants sporadic, in large part mono-podial and intercalary, but *robust plants sparingly and distantly to copiously furcate, terminally branched;* gynoecia regularly with 1-2 innovations. Stems robust, over 220-400 μ in diameter, over 12 cells high; cortex 2-3 stratose. Leaves typically very *densely imbricate, ovate-triangular to ovate-falcate in shape, ampliate, ca.* (1.3) 1.6-2.35 $\times$ as long as wide; postical leaf-margin showing a well-defined tendency to be undulate or crispate (at least on the bracts and subfloral leaves of female plants), with *postical base long-decurrent* (usually *ca.* 0.5-0.8 the merophyte length), *the decurrent strip erect, and crest-like, or reflexed and forming a postical pocket; leaf long-decurrent antically,* forming a sublinear, oblique fold. Cells $\pm$ strongly collenchymatous, *medium sized* (18-23 μ wide in leaf-middle); *basal vitta absent;* trigones large to bulging (only mod. *meso-* and *pachyderma* normally occurring in nature); oil-bodies 4-9 usually, up to 5.5 x 9 μ, coarsely to finely segmented, appearing *coarsely papillose. Underleaves distinct, large,* less often nearly obsolete, *divided into cilia or laciniae. Asexual reproduction by means of leafy propagula of the postical* (and more rarely also antical) *surface of the persistent leaves.*

Plants *frequently producing perianths,* but apparently rarely androecia. Perianths inflated below, distally compressed, the long dorsal keel 2-3 mm long, *usually much longer than the postical keel, the mouth thus* (in lateral view) *obliquely truncate, very broad,* often reflexed in part, *ciliate to ciliate-laciniate; dorsal keel usually at least narrowly winged,* sometimes dentate, postical keel apparently never winged. Androecia either terminal on leading shoots and becoming intercalary, or *often basal on the dichotomous forks of a leading* axis, the bracts closely imbricate, forming a compactly spicate androecium, similar to leaves in degree of postical decurrence and in the dentition of the margins, their basal 0.5-0.7 strongly concave, forming a conspicuous basal pocket.

This section, in the very long-decurrent postical crest-like or reflexed leaf-bases, occupies an isolated position. The more advanced species (*P. undata, P. miradorensis*) show no close relationship to other sections, but the less advanced (*P. ludoviciana*) often show much lesser development of the postical reflexed decurrent strip, and then clearly show a close relationship to the species of the previous section. Confusion with species of other sections is hardly possible, although juvenile plants may approach mature plants of the Sectio Contiguae. The separation of species of this section from those of the preceding (Sectio Hypnoides Carl) is often difficult. *P. ludoviciana,* a crista-bearing species, would go into the Hypnoides if we follow the concepts of Herzog (1932), even though placed as a primitive species of the Crispatae by the writer. Herzog (*loc. cit.*, p. 217) considers the two sections closely affined, stating "Es ist mir überhaupt sehr wahrscheinlich, dass Crispatae und Hypnoides eng zusammengehören." The writer suggests that species with a long-decurrent postical leaf-base (forming a sharp crista- or water-sac) be assigned to the Crispatae; species with a short-decurrent postical base, at best narrowly reflexed, are referred to the Hypnoides (see pp. 56, 68).

Herzog (*loc. cit.*) assigns such species as *P. undulifolia* to the Hypnoides; this species, as far as I can judge, is scarcely separable from our common *P. ludoviciana.* Similarly, *P. blepharobasis,* identical in leaf-form, in the virtually edentate margins, except for the short decurrence of the reflexed base, to *P. miradorensis* is placed in the Hypnoides, "oder vermittelt zwischen diesen und den "Crispatae" (Herzog).

The North American species of the Crispatae, and of the allied Hypnoides, have been extraordinarily confused in all the preceding literature. Twelve different species, mostly quite unrelated, have been found in herbaria (and in the literature) listed as "*P. ludoviciana.*" Inversely, good material of *P. ludoviciana* has been listed under several other names, as for instance, *P. undata* (Redfearn, 1952). Fully 75 percent of all herbarium specimens (and literature reports) of "*P. ludoviciana*" which have been seen refer to other species. Prominent among the misunderstood related species are *P. miradorensis* and *P. hypnoides,* which have not been previously reported from the United States, and *P. undata.* The latter species is so distinct that no reason exists to devote a discussion to its affinities and distinction. *P. hypnoides* also is nor-

mally easily distinguished. However, *P. ludoviciana* and *P. miradorensis* are closely allied, exhibiting variations which to some degree bridge the distinctions between them. The following essay on the variability of the *P. ludoviciana-miradorensis* complex, based on a three-month study of all accessible material, serves to elaborate some of the features in which these species approach each other, and to suggest points of distinction.

In addition to the great latitude of variation which the regional material exhibits, there is superimposed a bewilderingly wide amplitude of variation in the tropical members of the *P. ludoviciana-guilleminiana* complex. The concept of species limits here is fluid, needing to be hardened through extensive field experience and experimental work. Some of these problems are briefly discussed under *P. ludoviciana* (pp. 89-94). The immediately subjoined discussion is restricted to the members of the complex occurring in our immediate area.

Variation.—*P. ludoviciana* and *P. miradorensis,* as broadly delimited here, exhibit an extraordinary polymorphism. It is possible that several additional, closely allied species are involved. This appears to have been the conclusion of Gottsche (1863), who described a large number of "species" in this complex. However, as soon as a detailed analysis is made of a long series of specimens, the differences that initially appear so impressive almost disappear. Of more importance, systematically, is the fact that there is little or no linkage in the appearance of particular characteristics — each individual feature varying to a large extent independent of the others. As a consequence, if species are to be recognized at all in this complex, we must limit them to the two here recognized, or we would have to recognize infinitely more than the nine or ten "species" recognized in this complex by Gottsche for Mexico.

The polymorphism of *P. ludoviciana* and *P. miradorensis* occurs along a series of lines, including (a) variation in degree of decurrence of the postical leaf-base; (b) variation in leaf-shape; (c) variation in dentition; (d) variation in the form of the crista or of the "water-sac"; (e) variation in cell form and size; (f) variation in propagula formation; (g) variation in form of the ♀ bracts; (h) variation in form and dentition of the perianth; (i) variation in degree of development of the underleaves. The following analysis serves to document this polymorphism. It is to be noted that this analysis is based almost exclusively on regional material.

Variation in degree of decurrence of postical base[1]:— In all typical material of *P. ludoviciana,* the postical base is long-decurrent (0.6-0.75 the merophyte length, normally), the decurrent strip extending down (from the arched summit of the line of insertion) for a distance equivalent to 0.55-0.75 the length of the degree of decurrence of the antical half (again measured from the summit of the arched portion of the line of insertion) (Figs. 61:7; 62:1, 10). The antical half of the leaf is prominently long-decurrent (the line of insertion running

[1] Figs. 61-63 are intended to portray much of the gamut of variation in this complex, and should be referred to in this conjunction.

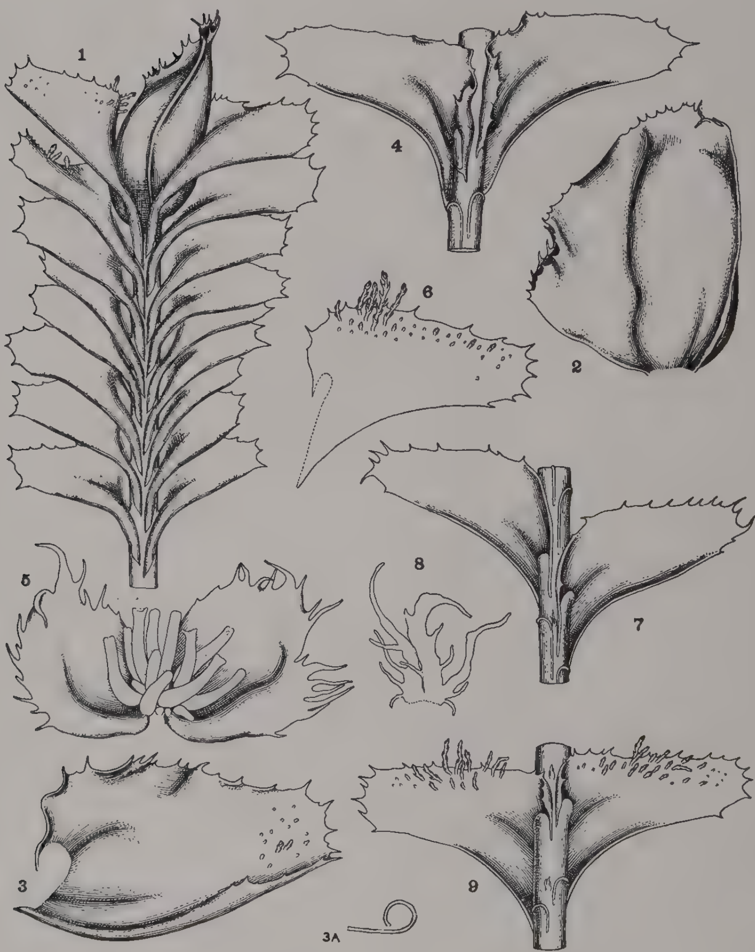

Fig. 61.—Sectios Hypnoides and Crispatae. 1-3, 7-8, *P. ludoviciana* Sulliv. 1. Shoot with perianth, with few propagula of adaxial leaf- and bract-surfaces (x 14); 2. Perianth, lateral aspect, keel at right (x 18); 3. Bract, abaxial aspect (x 18); 3A, the "cnemis," in cross-section, showing the strongly involute leaf-margin; 7. Shoot-sector, postical aspect, of mod. *angustifolia-dentata,* showing crista and postical decurrence (x 16); 8. Underleaf of maximal size (x *ca.* 30). 4, 5. *P. miradorensis* Gottsche. 4. Shoot-sector, postical aspect, showing convolute postical leaf-bases and decurrence (x 16); 5. Juvenile perianth, atypical, opened to show archegonia. 6, 9. *P. hypnoides* Lindenb. 6. Leaf with propagula, postical aspect (x 14.5); 9. Shoot-sector, with propagula, postical aspect, showing crista and short decurrence (x 16). (Figs. 1-3, near Chunchulla, Alabama, *Schuster* A-109; 4-5, NW. of Brooksville, Fla., *Schuster* 22075a; 6, 9, Paradise Key, Florida, *Schuster* 20295a; 7, *Schuster* 22975.)

down for a distance of *ca.* 760-950, occasionally 1050-1100 μ; this line equal to *ca.* 0.8-1.0, the maximal leaf-width just above the base). As a consequence the degree of decurrence of the postical base varies from *ca.* 475-575 μ. However, in weak forms, or on weak stems, the degree of decurrence may be much less, and such relatively short-decurrent, juvenile manifestations may approach *P. hypnoides* in this respect. The adult phases of these two species, however, differ greatly in the degree of decurrence (compare, *e.g.*, Fig. 61:7 and 9). Some of the considerable confusion existing in the *P. ludoviciana - guilleminiana* complex is attributable to the variation in degree of decurrence that exists between normal or optimal forms of the same species, and between small plants exhibiting juvenile features. Often differences are exhibited on individual stems that are suggestive: the lower, more juvenile leaves showing a lesser degree of decurrence than the upper, normal leaves. As a consequence, observations need to be restricted to mature, normal portions of leading stems or main branches, on which *P. ludoviciana* always exhibits the characteristic, markedly elongate postical decurrence diagnostic of the species.

In *P. miradorensis* the degree of decurrence postically is perhaps very slightly less extensive, rarely extending down for as much as 0.75 the merophyte length (Figs. 61:4; 62:7; 63:5). In the extremely slender-leaved forms with entire leaves (mod. *angustifolia-integrifolia*) the postical base is much less developed, and considerably less decurrent. The decurrence here ranges usually from 0.4-0.5 the merophyte length, only exceptionally to 0.6 this distance (Fig. 69:3, 5). The plants of this extreme also bear relatively short-decurrent antical leaf-bases (Fig. 69:4), and are probably genotypically distinct from *P. miradorensis*, s. str.; they are here described as var. *convoluta*.

Variation in leaf-shape.—The leaf of *P. ludoviciana* varies from obliquely and broadly ovate-triangular (type; Fig. 63:2), with the maximal length 1.3-1.5 × the leaf-width, to narrowly ovate-rectangulate. In the latter case, the leaf may be only very slightly ampliate (Fig. 66:13), with the length equal to 1.75-2.25 × the maximal width; such extremes are relatively rare, however. The minor variations of the preceding type of leaf-form share in common a nearly straight antical leaf-margin. The postical margin, by contrast, is usually at an 85-95° angle with the stem. *P. ludoviciana,* therefore, can be characterized as possessing a limited range of variability as regards the leaf shape. By contrast, in *P. miradorensis* we find an extraordinary diversity in leaf-shape. The leaves range from lanceolate-falcate to ovate-falcate or oblong-falcate to (rarely, and perhaps abnormally) shortly oblong. In the case of the "normal" ovate-falcate type, the antical leaf-margin is visibly arcuate (Figs. 68:6; 62:7), and the postical leaf-margin may be at an angle of 95-110° with the stem. In these cases, the length of the leaf usually ranges between the extremes previously given: *i.e.*, from 1.5-1.75 × the maximal width.

In more extreme cases, the leaf of *P. miradorensis* becomes 2.0-2.35 × as long as wide, obliquely lanceolate-falcate, with the distal portion

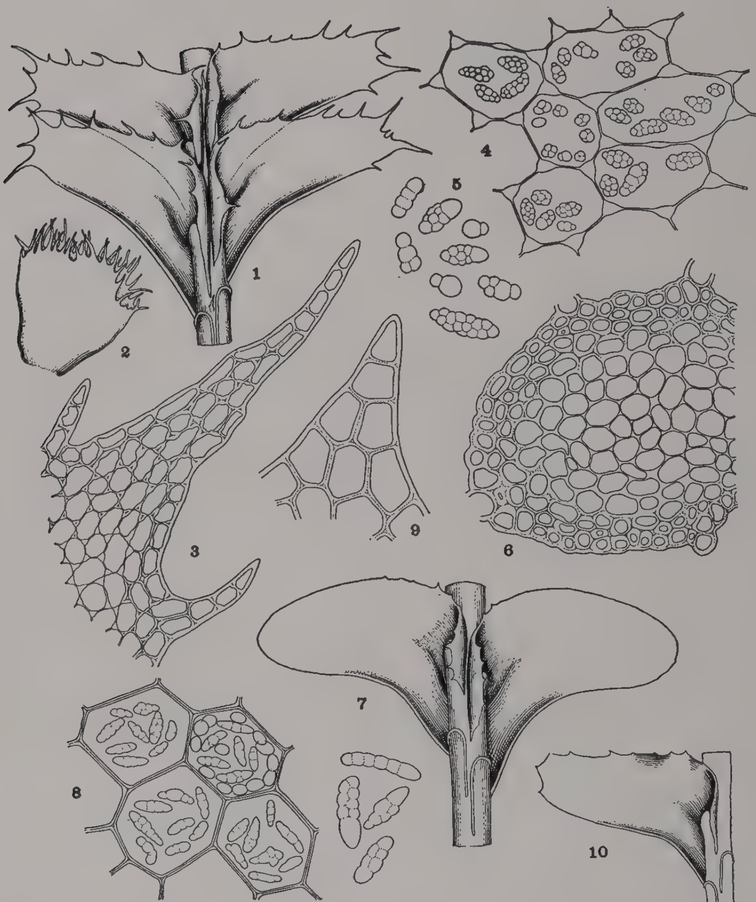

Fig. 62.—Sectios Hypnoides and Crispatae. 1-3, 8-10. *P. ludoviciana* Sulliv. (in 1-3, mod. *spinosissima;* in 8-10, mod. *integrifolia-viridis-leptoderma,* the *"P. tunarum"* extreme). 1. Shoot-sector, postical aspect (x 25); 2. Juvenile perianth, lateral aspect (x 16.5); 3. Leaf-apex, the middle tooth one of the large apical teeth (x 177); 8. Median cells with oil-bodies (x 560), at right individual oil-bodies (x 950); 9. Marginal tooth near leaf apex (x 345); 10. Leaf, *in situ,* postical aspect (x 14.5). 4-5. *P. hypnoides* Lindenb. 4. Median cells with oil-bodies (x 485); 5. Individual oil-bodies (x 865). 6-7. *P. miradorensis* Gottsche. 6. Stem cross-section (x 150); 7. Shoot-sector, postical aspect (x 16.5). (Figs. 1-3, *Schuster* 22987, Van Cleave, Miss. [see also Fig. 66:17-20]; 4-5, *Schuster* 26018, Highlands Hammock, Fla.; 6-7, *Whitehouse* 23318, Texas [see also Fig. 68:10-15]; 8-10, *Schuster* 26125, Collier-Seminole State Park, Fla.)

of the leaf prominently drawn out (Fig. 67:6-7, 14, 16). This extreme has been found occurring on the same plant (indeed, on the same shoot!) with the opposing extreme (Fig. 67:11, 12,18), in which the leaf is short-rectangulate and very wide, broadly rounded distally, strongly undulate, and only 1.3-1.4 × as long as wide. The shoots (or shoot-sectors) with this form of leaf closely simulate those of *P. undata* in many respects, and may be confused with them.

In general, however, *P. ludoviciana* has a more ovate-triangular leaf, with a nearly straight antical margin, while *P. miradorensis* has a narrower leaf, with a curved antical margin, the leaf being more drawn out, and clearly somewhat falcate. Usually the two species are separable at sight, on this basis. However, extreme forms of *P. ludoviciana* occur (Fig. 65), here tentatively separated as the var. *invisus,* in which we find a more attenuated leaf, *ca.* 1.85-2.0 × as long as wide, with a somewhat more falcate form than is "normal" in *P. ludoviciana.* The leaves in this case are also unusually strongly ampliate above the postical base (Fig. 65:6-8), and tend to have a strongly undulate crista, occasionally reflexed to a greater than normal degree (Fig. 65:1). Such plants serve to break down some of the value of a distinction between *P. ludoviciana* and *P. miradorensis.*

The sum total range within each of these two species thus goes from a leaf length of 1.3-2.25 × that of the leaf width, *on mature leaves.* On immature leaves, the width is proportionately greater. However, the variation in measurements given here cannot be regarded as due to allometric growth, since they are derived largely from plants of similar size (compare Fig. 66:5 and 13).

Variation in dentition of the leaves.—Typically, in *P. ludoviciana* the leaf-margins bear only 10-15 marginal teeth (7-13 *fide* Frye and Clark, p. 455, but this figure is certainly too low), as is the case in Sullivant's type material; these teeth are furthermore relatively small (4-6 cells long usually), except the two lobe-like apical teeth that are usually distinct, and which may be much larger.

In extreme forms, in which the plants are not at all luxuriant (female plants *ca.* 2.1-2.3 mm wide), an extreme development of marginal teeth of the leaves may occur, the longest, spinose ones being 10-12 cells long x 3-4 cells wide at base (Figs. 66:17; 62:1, 3); the teeth may be fewer, though, than in the other types, averaging 9-12 or 12-17 per leaf (as in *Schuster* 22987, Van Cleave, Miss.).

At the opposite extreme from these last two types is a form with the leaves entire or virtually so. The plants, though robust (*ca.* 3.5-3.8 mm wide) and with long-decurrent postical bases (which are distinctly cristate), show 0-3 (5-6) small teeth on the distal portions of the leaves, 0-5 on the postical margins and none on the postical, cristate bases (Fig. 68:22).

Careful field study suggests that in *P. ludoviciana* the notably coarse and strongly spinose teeth which are usually developed tend to be reduced, or even almost eliminated, when 1) the plants grow in excessive shade, and 2) they grow under unusually humid conditions. In such cases, the leaves retain a juvenile facies. (Immature leaves in this species are commonly quite edentate). Inversely, in at least some cases we find that plants growing under relatively xeric condi-

tions, in more direct light, tend to have strongly spinose dentate leaves (Fig. 62:1, 3). However, this is far from universally the case.

Preliminary study suggests that there are two such genetically controlled patterns of variation in the *P. ludoviciana-miradorensis* complex, each subject to some environmental modification. In the type plants (Fig. 63:2-3), and almost all other material seen of true *P. ludoviciana* (Figs. 64-66), the postical leaf-base, and the margin for some distance above the base, tend to be essen-

Fig. 63.—Sectio Crispatae. 1, 4-5, 10. *P. miradorensis* Gottsche. 1. Median cells with oil-bodies (x 550); 4-5. Antical and postical aspects of shoot-sectors, in 5 with minimal decurrence (x 12.5); 10. Sector of plant, antical aspect (x 12.5); 2-3, 6-9, 11-12, *P. ludoviciana* Sulliv. 2. Shoot-sector, postical aspect (x 12); 3, 7-8, 11. Leaves (x 13); 6. Lateral aspect of shoot-sector, with distal parts of leaf removed, showing insertion (x 13); 9. Shoot-sector, postical aspect (x 13); 12. Large underleaf (x 17). (Figs. 1, 4-5, *Schuster* 19184, n. of Escatawpa, Miss.; 10. *Schuster* 22110a, near Brooksville, Fla.; 2-3, 6-9, 11-12, from type of *P. ludoviciana* [see also Fig. 66:1-4].)

tially edentate, *while the teeth are developed with increasing robustness towards the leaf apex.* Inversely, in shade or weak forms of this type, the teeth are retained, or tend to be retained, at the leaf-apex, those in the basal half of the leaf being "lost" first. In the second type of plant, referred here to *P. miradorensis* (Figs. 68, 69), the *degree* of development of the teeth is reversed; the postical decurrent area retaining sharp, spinose teeth at nearly all times, while the distal portions of the leaves are edentate or virtually so (Figs. 62:7, 68:16), or may bear relatively low, scarcely spinose teeth (Fig. 68:1). Only in extreme cases do the plants of the *P. miradorensis* type lose the cilia or teeth of the postical leaf-base.

Of considerable interest is the fact that these two differing modes of dentition are correlated with the following character:

Variation in form of the crista or water-sac.—In the type plants of *P. ludoviciana* (Fig. 63:2, 9), and most other collections studied referable to this (Figs. 64-66), the decurrent postical "strip" is narrow and nearly or quite edentate; it is, furthermore, erect or squarrose rather than convolute. Consequently, in these plants there is formation of a crista (Figs. 61:7, 63:2, 9), or in the aggregate, an erect line of crests on the postical face of the stem (Fig. 64:6). Such a modification occurs to a lesser degree in the related *P. hypnoides.* In a minority of the regional plants examined, referred to *P. miradorensis,* the decurrent base is sharply reflexed or even distinctly convolute, forming a distinct "pocket" or water-sac in extreme cases (Figs. 61:4, 62:7, 67:16, 18). In such cases there is always correlated a development of 1-several sharply spinose teeth (on at least some leaves) of this basal, convolute region.

It has been customary in the literature (*e.g.,* see Herzog, 1932; Carl, 1931; Gottsche, 1863) to regard the plants developing only a "crista" as distinct specifically from those with a basal "pocket." The association of a different pattern of distribution of the marginal teeth (see above) suggests that these workers are correct in such an evaluation. However, study of a series of specimens shows that intermediate forms occur, which are clearly derived from *P. ludoviciana.* For instance, in *Schuster* 22975 (Fig. 64) the decurrent strip is usually edentate, but occasionally bears a single tooth; the crista here is narrowly reflexed. In *Schuster* 22987 (Fig. 66:17), the postical base may bear (0)-1-3 sharp teeth, on the most robust leaves (usually on fertile plants); in such cases it is distinctly, if not broadly reflexed, foreshadowing the "pocket" developed in true *P. miradorensis.* The occurrence of such leaves at first glance would almost invalidate any attempt to separate the present complex on the basis of the "presence" *vs.* "absence" of a postical "water-sac." In the less robust shoots of this collection (*e.g., Schuster* 22987) the postical base is in the form of a crista, and the crista is edentate or rarely bears a single sharp tooth. In such cases the resemblance to the uniformly cristate leaves of *Schuster* 22975 becomes remarkable. The similarity of these two plants in other respects is also remarkable: for instance, compare the densely ciliate perianth-mouth (Figs. 62:2; 64:7); the thick-walled, narrowly rectangulate cells of the postical leaf-base (Figs. 64:9, 66:18); the similar cells of the leaf-apices, with the marginal and apical cells tending to be rectangulate and somewhat elongated (Figs. 64:11; 66:20). The conclusion is inescapable that the plants of these two collections are very similar genetically, if not virtually identical.

A careful study of such plants, with some leaves bearing 1-2-3 teeth of the

postical bases, shows that, in spite of this deviant feature, they belong to *P. ludoviciana.* They resemble the latter (and differ from *P. miradorensis*) in several respects: (1) the leaves are sharply spinose-dentate in the distal half; (2) the postical decurrent base, dentate or edentate, is formed of prominently elongated, rectangulate cells with their longitudinal walls strongly thick-walled (due in part to confluence of the trigones); (3) the leaves are more ovate-triangular, with a nearly straight antical margin, on flattened leaves; (4) the ± elongate cells of the leaf-apices have the longitudinal (tangential) walls of the marginal several cell-rows ± thick-walled.

The considered conclusion of the author, then, is that the form of the postical leaf-base warrants a separation of what has, in our area, passed as *P. ludoviciana* into two distinct species.

Variation in cell form and size.—P. ludoviciana usually occurs as the mod. *pachyderma,* with the cells bearing bulging trigones (and, in the basal median cells, scattered intermediate thickenings on the longer walls). The cells of the apex, and on the margins, tend to become somewhat, but never prominently, elongated parallel to the leaf-margin; they furthermore are often ± thick-walled, parallel to the margins with the consequence that the trigones become nearly obliterated. The secondary thickening is developed largely on the walls parallel to the leaf-margins. This is particularly prominently the case, in many phases, in the area near the postical, decurrent portion of the leaf (Fig. 66:10, 18); the cells in such cases may be perfectly rectangular and average 10-12 (13) x (35) 40-50 μ in length. In less extremely xeromorphic phases, the cells of the postical base appear less elongated (Fig. 66:2, 6), and show confluence of the trigones to a lesser extent.

The previous manifestations (see Figs. 64; 66) show how polymorphic the pattern of wall-thickening may be in this complex, even in "normal," pachydermous phases. In all these cases, the median cells, and those at median base, are clearly provided with coarsely bulging trigones. In the extreme shade forms of *P. ludoviciana,* the trigones may be much reduced everywhere in the leaf. In the most extreme case seen, the walls are very slightly equally thick-walled, without trace of trigones. In all these various types, the basic dimensions of the cells remain essentially unchanged, although the proportions of the cells near the postical leaf-base are quite radically different in *P. ludoviciana* and *P. miradorensis.* In the most extreme phases, the mod. *integrifolia-leptoderma,* the cells of the postical base are only slightly differentiated, averaging only 1.5-2.5 $\times$ as long as wide (Fig. 65:11-12). In such cases, the walls are not or little thickened (and the longitudinal walls are not differentiated from the shorter cross-walls). Such cases are relatively rare, and it seems warranted to consider the tendency for formation of a basal area of narrow, rectangulate cells as a "normal" manifestation in *P. ludoviciana,* hence of systematic importance. The form of these cells of the postical base emerges most clearly when they are compared to those of the median base of the leaf (cf. Figs. 64:9, 10; 65:12, 13; 66:10, 11; 66:18, 19; 67:3, 4).

In contrast to this differentiation of a postical region of elongated cells stands the simpler condition in *P. miradorensis.* In this species the cells of the postical flap are collenchymatous exactly like the median basal cells — *i.e.* bear nodose trigones, which are sharply defined

and not confluent. Consequently, the basal cells never develop equal, strong, longitudinal walls. Furthermore, the basal cells are more nearly isodiametric (Figs. 67:10; 68:3, 7, 12, 18). In the forms with a relatively narrow, edentate postical flap (var. *convoluta*), the cells may be slightly elongated, and twice as long as wide.

Variation in propagula formation.—Normal manifestations of *P. ludoviciana* and *P. miradorensis* are always abundantly propaguliferous. However, under extremely shaded conditions (as in the deepest, permanently shaded portions of hammock forests, with a light intensity never exceeding 12 foot candles) and under unusually moist conditions (as along streams), *P. ludoviciana* may be habitually without propagula. Furthermore, such extreme shade (and/or high moisture) forms also show a high level of reduction of the dentition. On these two bases, such forms may be confused with *P. undata*. However, all such phases of *P. ludoviciana* seen show formation merely of a crista —never of the reflexed, convolute basal region characteristic of *P. undata*. Leptodermous, propagula-free phases of *P. miradorensis* have not been seen.

It should be emphasized at this point that the immediate relatives of *P. ludoviciana* found in the wet montane rain forests of the Cordilleras of South America, and in the dense tropical rain forests of that continent, normally fail to exhibit any trace of propagula. It is hypothesized that either the plants must occur in exposed areas with at least intermittently high saturation deficit, or in areas with a good deal of insolation, or both, before propagulum development is initiated.

Variation in form of the female bracts.—The female bracts of the *P. ludoviciana* complex undergo almost as wide a series of variations as do the vegetative leaves. Furthermore, the variation is usually clearly parallel to that of the leaves. This is clear when we compare the leaves (Fig. 66:5) with the bracts (Fig. 61:1, 3) of one of the less extremely dentate forms, in which the postical leaf-base is always entire (*Schuster A*-109). The leaves here bear *ca.* 9-18 rather moderate-sized or small teeth, and the leaf averages *ca.* 1.5-1.6 × as long as broad. The bracts in this case average *ca.* 1.5 × as long as broad, and bear rather moderate-sized teeth, 24-28 per bract. If a sharply spinose-dentate phase is studied (Figs. 62:1, 3; 64:1; *Schuster* 22975, 22987) the leaves are seen to bear 10-18 longer, more jagged teeth; the leaves average 1.6-1.9 × as long as broad. In such cases the corresponding bracts average 1.6-1.9 × as long as broad, bear sharper, more uneven, jagged teeth (often more numerous, ranging to 36-45 per leaf; see Fig. 64:2-3).

On the other hand, phases with subentire leaves (var. *invisus;* Fig. 65:1, 2) may have the bracts coarsely dentate. In the illustrated case, note that the ampliate postical base is particularly coarsely dentate, although the teeth are unusual in their irregular form and disposition, and in being scarcely sharp at the summit. The two bracts (Fig. 65:9-10) shown also illustrate the great variability in development of teeth of the antical leaf-margin.

The antical, convolute margin of the bracts may bear only 2-3 teeth near its apex (Fig. 64:3); in other cases the teeth may extend down to the basal third of the bract, and number 4-6 along the antical margin (Fig. 65:9). Study of the excellent figures given by Gottsche (1863) of the female bracts of the various species he described (here listed in synonymy under *P. ludoviciana*) indicates an even more extensive range of variation. In particular, some of the plants figured by Gottsche possess female bracts whose antical margin is spinose-dentate to the base. This only rarely occurs in our plants of *P. ludoviciana,* and then the antical teeth are small.

In *P. miradorensis* the bracts, like the leaves, tend to be more strongly attenuate. The bracts vary from 2400-2700 μ long x 1050-1350 μ wide, gradually tapering to a width of only 350-450 μ before the somewhat truncated apex. The antical margin is strongly convolute, and may bear obscure low teeth to within the basal third of the margin. The postical base (which tends to be convolute) and margin bear spinose teeth, which become progressively less sharp and marked towards the 3-4-dentate apical portion of the leaf. The postical base, on the antical margin, may bear isolated lamellate teeth (Fig. 70:1,3).

Study of a series of female bracts thus appears to demonstrate that (a) their dentition, in both species, tends to be coarser and more ample than that of vegetative leaves; (b) *P. ludoviciana,* even in attenuate-leaved extremes like the var. *invisus,* has relatively short female bracts, never twice as long as wide; (c) *P. miradorensis* has the female bracts strongly drawn out, like the leaves, and fully twice as long as wide. This difference in shape of the bracts is probably of systematic value.

Variation in form and dentition of the perianth.—Although neither androecia nor gynoecia of *P. ludoviciana* have been described, gynoecia are frequently produced. The writer, however, has seen only a few androecial plants. Gottsche (1863) has described the perianths of several of the Mexican "species" here regarded as identical with *P. ludoviciana.* Although gynoecia are rather frequently developed, fertilized archegonia have never been seen. Associated with this, it is customary to find only rudiments of the perianth.

Archegonial plants of both *P. ludoviciana* and *P. miradorensis* (cf. *Schuster* 22085a), at time of maturation of the archegonia, do not show any trace of a recognizable perianth. The archegonia are surrounded by a pair of presumably perichaetial bracts, completely free at the base, which are less than one-half the length of the leaves, but strongly ciliate from their middle upward (Fig. 61:5). These bracts are only *ca.* 600 μ long, broadly suborbicular to obovate and are strongly ventricose and closely approximated (with the archegonia thus in a chamber formed by them, and completely hidden from view). The archegonia number *ca.* 12 (with several rudimentary ones); at time of their maturation there is no trace of a true perianth at their base. In almost every case seen, correlated with the cessation of growth of the shoot subsequent to initiation of archegonia, a single lateral innovation developed below the archegonial group (in the axil between the putative perichaetial bract and the normal vegetative leaf below it).

With study of further collections (*Schuster* 22975), it becomes evident that

the putative perichaetial bracts of the previous collection (*Schuster* 22085a) are really equivalent to the undeveloped, deeply bilabiate, perianth. In the material of *Schuster* 22975, plants with postmature archegonia, surrounded by a pair of short, broadly obovate bracts are rather common. In this case, however, the broad and short ciliate bracts are "fused" postically to a slight extent (0.2-0.4 their length) but fused nearly their entire length dorsally, thus constituting a real perianth. Their distal, free margins are closely ciliate much as are the margins of the free bracts. It is thus evident that, without fertilization, a perianth may or may not be formed in this species — depending on whether the two bracts homologous with the perianth are connate dorsally and ventrally or not. When connate, the point of union dorsally is sharp, and may be very narrowly winged, while the shorter line of fusion ventrally is not perceptibly winged. In *Schuster* 22975, as in the previous collection, the development of archegonia results in most (but not all) cases in the development of an innovation directly below the perianth. A plant where such innovation does not take place is shown in Fig. 64:1. It is of some interest to note that fertile archegonial plants may be freely propaguliferous (as in *Schuster* 22975), leaves immediately below the perichaetial bracts bearing propagula.

In only a few cases have I been able to find what may be considered mature perianths. These, however, may be produced without fertilization having taken place. Since the species, in our area, consists almost wholly of populations of the female sex (or else includes male populations unable to produce androecia), it seems improbable that mature perianths are frequently produced.

However, in a series of collections, all uniformly female, the mature perianth appears to be developed — without previous fertilization having taken place (the archegonia being largely disintegrated). The formation of perianths here did not appear to result in any inhibition of propagula formation - even the perichaetial bracts showing propagula, on both upper and lower leaf-surfaces.

In these exceptional cases, where mature perianths were developed, the perianth mouth is rather shortly ciliate-dentate, with the teeth quite similar to those of the leaves and bracts; the teeth are furthermore, relatively remote from each other (Fig. 61:1, 2). In the several instances where immature perianths were found, the perianths were generally closely ciliate, with slender, uniseriate cilia (Figs. 64:7, 8; 62:2). This range of variation in degree of development of the cilia appears impressive at first. It must be kept in mind, however, that this is correlated to some degree with differences in degree of dentition of the leaves. Plants with sharply spinose-dentate to spinose-ciliate leaf-margins have the perianth-mouth ciliate to ciliate-laciniate. Inversely, plants with rather finely dentate leaves appear to have the perianth mouth relatively finely and distantly dentate or spinose-dentate. This correlation is far from uniform. In the attenuate-leaved var. *invisus* (Fig. 65) the leaves are almost entire-margined, but the immature perianths seen were densely and strongly ciliate-laciniate (Fig. 65:3-4). Preliminary studies thus suggest that the differences in dentition of the perianth-mouth are of minor systematic significance, but, admittedly, study of longer series of female plants may show cor-

relation of differences in this feature with other more significant characters.

The form of the perianth also appears somewhat variable. The mature perianths seen were clearly asymmetrical, in lateral view, with the antical keel about twice the length of the postical (Fig. 61:1, 2). In these cases, the area adjacent to the postical keel was compressed, that adjacent to the antical keel, inflated (except at the mouth). The juvenile perianths show, in some cases, a similarly abbreviated postical keel (Fig. 64:7), but in other cases the postical keel is only slightly shorter than the antical. A similar variation characterizes the Mexican plants illustrated (under a variety of species names) by Gottsche, although the perianth mouth in these is rarely as extremely obliquely terminated as in Fig. 61:2.

In almost all cases seen, the antical keel of the perianth, which never appears to run up to the summit of the perianth, is very narrowly winged, and the wing gradually disappears above. Only in *P. ludoviciana* var. *invisus* does the antical keel ever suddenly end in a distinct tooth (Fig. 65:3).

P. miradorensis appears to be extremely similar to *P. ludoviciana* in regard to the perianth. The mature perianth is essentially identical to that of *P. ludoviciana,* with the antical keel longer than the postical, and with the compressed lower portion of the mouth tending to be reflexed. Gottsche (*loc. cit.*) has figured the perianth of the type of *P. miradorensis* as having a well-developed antical keel, bearing several teeth. The mature perianths seen (*Schuster* 19250b) agree in this respect with Gottsche's type, and with the few other Floridian collections seen bearing immature perianths. The little perianth-bearing material seen of *P. miradorensis* shows a narrower range in dentition of the mouth than that so far found in *P. ludoviciana.*

The highly similar perianths of *P. ludoviciana* and *P. miradorensis* thus show only one difference of any systematic value: the antical keel of the perianth of the former species tends to be short and edentate, at most ending in an obtuse tooth, while in *P. miradorensis,* the longer antical keel bears 2-4 teeth; the latter may be low and inconspicuous.

Variation in the degree of development of the underleaves.—The *P. ludoviciana-miradorensis* complex always possesses at least vestigial underleaves. These appear to have been overlooked in a few of the plants described (as separate species) by Gottsche, from Mexico; *e.g.,* in *P. schliemiana* var. *b.* The degree of development of the underleaves is subject to a very great degree of variation, as was noted as long ago as 1896 by Evans. In some populations they consist of a few cilia, free almost to base (Fig. 69:6-7), in other cases, of a small lamellate base, divided distally into several long cilia (Fig. 67:15) in still other cases they are larger, and divided almost to base into 2-several acuminate, tortuous laciniae and/or cilia (Figs. 65:5; 68:22).

An analysis of the variation-pattern in the underleaves allows a distinction of two fundamental types: (a) underleaves consisting basically of 2-several long tortuous cilia, which are uniseriate for their whole length, or perhaps 2-3 cells wide at base; (b) underleaves consisting of usually 2 linear-lanceolate laciniae, ending in a uniseriate row of cells, but 4-8 cells wide for much or most of their length, and

clearly united basally into a broad if short lamella; in addition to the 2 linear-lanceolate segments, secondary, shorter and narrower cilia or laciniae are normally produced. The first type of underleaf is correlated with the attenuate-leaved plants bearing a basal "pocket," *i.e.*, with *P. miradorensis*-like plants. The second type is always characteristic of plants with merely cristate bases, *i.e.*, with *P. ludoviciana*-like plants.

This distinction into two modes of variation breaks down in the exceptional cases where *P. ludoviciana* has rudimentary underleaves. These then may consist of short laciniae that are so narrow as to approach the cilia of *P. miradorensis* (Fig. 66:17).

There is no necessary correlation between robustness and degree of development of the underleaves. In some of the weaker forms, with obscurely dentate leaves, of shaded damp sites (*P. ludoviciana* var. *invisus*) the underleaves may be extremely large and well-developed (Fig. 65:5-7). Inversely, robust plants may have the underleaves so reduced that they are almost impossible to demonstrate (Fig. 61:7).

This absence of any obvious correlation between size of the plant and underleaf size is particularly well-marked in the tropical plants, from South America, which are either conspecific with *P. ludoviciana*, or else so closely allied as to be hardly separable, *e.g.*, *P. guilleminiana*, *P. oreocharis* and *P. rhizophila*. These taxa are discussed under *P. ludoviciana* (pp. 89-94). In them we may find robust plants, 4-5 mm wide and to 4-6 cm long or more, in which the underleaves are almost vestigial. The longly decurrent postical bases of the leaves are here closely juxtaposed, hence the ventral merophytes have been perceptibly narrowed. It is still questionable to what extent the relative reduction of the ventral merophytes is a valid criterion in the distinction of species. I have, tentatively, considered such variation intraspecific, especially since it does not appear linked with other diagnostic features. This matter, however, needs much more, and careful, future investigation.

The preceding analysis and accompanying illustrations have shown that the *P. ludoviciana-miradorensis* complex (as represented in our area) shows a bewildering degree of variability. Some of the extreme variations can probably be largely or entirely attributed to environmental stimuli; others appear to be genetically determined (with a limited amount of environmentally-induced variation superimposed). At present it is almost impossible to separate these two sources of variability. As a consequence, the recognition of varieties within the species (and/or recognition or segregation of additional species from the complex) appears unwarranted, with few exceptions. The following summary, in key form; analyzes some of the most significant variations which the writer has found in our material. For the presumably environmentally-induced variation the terminology of Buch (*i.e.*, the term "modificatio") is used. *P. undata* is not included in this key since its strongly crispate leaves serve to separate it from the other taxa treated here. In the key *P. hypnoides* is included, owing to the fact that it has been universally confused, in the North American literature and herbaria, with the *P. ludoviciana-miradorensis* complex.

KEY TO SPECIES AND VARIATIONS IN SECTIO HYPNOIDES AND SECTIO CRISPATAE

1. Leaves with postical base prominently long-decurrent on mature shoots, the decurrent strip running down for (0.45) 0.55-0.85 the merophyte length, and for *ca.* (0.45) 0.55-0.75 the length of the decurrence antically. 2

2. Postical base erect, not reflexed or convolute, edentate (rarely with 1-2 teeth), forming a crista, relatively narrow; leaves with dentition tending to be reduced in basal half of leaf: the decurrent base without discrete spinose teeth, the apex almost always ± dentate or spinose-dentate; underleaves normally formed of 2-several laciniform, tortuous lobes (each 3-several cells broad at base). Cells of decurrent postical strip ± rectangulate, (1.5) 2-5 × as long as wide; cells in leaf-apex (near margins) tending to be elongated parallel to margin. *P. ludoviciana* Sulliv. 3

3. Leaves ± sharply spinose-dentate, at apex usually with 2-3 (> 5) very coarse apical teeth, the postical margin usually with 5-10 less coarse teeth; cells ± strongly collenchymatous; propagula freely produced; underleaves small to large: their length rarely approaching the leaf-width. 4

4. Leaves relatively broad: averaging 1.35-1.55 × as long as wide; postical, decurrent strip and area immediately above it, formed of ± collenchymatous cells averaging 1.5-3 (4) × as long as wide; perianth-mouth rather shortly, irregularly laciniate-dentate; teeth of leaves relatively coarse and short, obtuse to acute, broad-based. (Mesic phase?) Typical phase ....(Mod. *latifolia-dentata*).

4. Leaves slender and elongate: averaging (1.65) 1.72-2.0 (2.2) × as long as wide; postical decurrent strip and area above it of prominently thick-walled cells (the longitudinal walls often undulate), averaging 3-5 × as long as wide; perianth mouth densely, longly ciliate with predominantly uniseriate cilia; teeth of leaves slender, acute to spinose, 1-2 (3) cells wide x 3-8 cells long, or longer. 5

5. Leaves with the dentition confined strictly to distal ¾ of the leaf, the postical base uniformly edentate; postical base never reflexed to any degree; teeth of distal half of leaf moderately spinose, 1-2 (3) cells wide x 3-8 cells long usually. ....Mod. *angustifolia-dentata*

5. Leaves (or some of them) with dentition extending down to the decurrent postical base, the base then with 1-2 (3) small but spinose teeth; postical base often somewhat reflexed, but never convolute; teeth of distal half of leaf strongly spinose, 2-5 cells wide x 8-12 cells long. ....Mod. *angustifolia-spinosissima*.

3. Leaves entire to subentire, the apex commonly with 2-3 low, obtuse remnants of teeth, the postical margin entire or rarely with isolated low teeth; cells never with strongly bulging trigones, the walls ± thickened; propagula absent; postical decurrent strip of little elongate cells (1.5-2.5:1), their walls not prominently thickened. 6

6. Leaves broad: averaging 1.35-1.6 × as long as wide on mature shoots; plants shiny in texture; underleaves vestigial, less than 0.3 the leaf-width in length. ....Mod. *leptoderma-latifolia-integrifolia*.

6. Leaves slender, somewhat falcate: averaging 1.85-2.1 × as long as wide; plants dull; underleaves large, often 0.7-1.0 the leaf-width

in length. ....
.............var. *invisus* var. n. = Mod. *leptoderma-angustifolia-integrifolia.*

2. Postical base distinctly dilated, broadly reflexed, the reflexed margin ± distinctly involute (the base thus ± tubular), the margin of the thus-formed pocket usually with (0) 1-6 sharp cilia or teeth; leaves with distal halves bearing small, low regular teeth (sometimes reduced to 1-several very small or obscure teeth; in many cases absent, or reduced to 1-2 apical teeth); underleaves normally formed of 2-several uniseriate, tortuous, long (sometimes branched) cilia, which are free virtually to base; cells of decurrent, reflexed leaf-base isodiametric or little elongated (length 1-1.8:1 usually), the cells collenchymatous like other leaf-cells; cells in leaf-middle, and in apex, as well as marginal cells almost uniformly isodiametric, the marginal collenchymatous like inner cells (never forming a thick-walled border). *P. miradorensis* Gottsche. 7

7. Postical leaf-bases relatively broadly reflexed-convolute, the border of the reflexed region usually 2-6-ciliate or dentate; leaves long-decurrent postically and antically: postical decurrence ranging from 0.55-0.75 the merophyte length; leaves usually ± dentate in distal halves. (*P. miradorensis,* typical). 8

8. Leaves regularly dentate, the teeth low but discrete, usually 8-16 above the postical reflexed base; leaves very narrow and falcate: 2.0-2.35 × as long as wide. ....Mod. *angustifolia-dentata.*

8. Leaves with apex rounded, truncate-bidentate, or ending in a single tooth, occasionally with a few obscure teeth elsewhere on postical margin; leaves broader, less than 1.85 × as long as wide. ....Mod. *latifolia-integrifolia.*

7. Postical leaf-bases narrowly reflexed-convolute, the reflexed border 0-1 dentate usually; leaves short-decurrent antically and postically: the postical decurrence ranging from 0.4-0.55 the merophyte length usually; leaves very narrow, 2.0-2.2 × as long as wide, entire-margined (except for 1-3 small apical teeth). ....
.................*P. miradorensis* var. *convoluta* (Mod. *angustifolia-integrifolia*).

1. Leaves with postical base short-decurrent on mature shoots, the decurrent strip running down for 0.2-0.35 the merophyte length, and only for 0.2-0.35 the length of decurrence of the antical portion of the leaf; postical leaf-base dilated, erect or nearly so, forming usually a distinct crista, never reflexed-convolute; leaf-margins always sharply and rather regularly spinose-dentate, the teeth (on mature leaves) extending down virtually to the postical base; underleaves lamellate, sometimes lobed, the margins bearing usually short cilia or teeth, rarely divided into several laciniae. ....
....*P. hypnoides* Lindenb.

PLAGIOCHILA LUDOVICIANA Sulliv.

Figs. 61:1-3, 7-8; 62:1-3, 8-10; 63:2-3, 7-9, 11-12; 64-66; 67:1-5; 68:22-25

? *Plagiochila guilleminiana* Montagne, *in* Lindenberg, Spec. Hep., 152, 1844; Herzog, Svensk Bot. Tidskr. 46(1):70, figs. 5-9, 11d, 12a-b, 1952.

? *Plagiochila rhizophila* Spruce, Trans. and Proc. Bot. Soc. Edinburgh 15:495, 1884-85; Herzog, Svensk Bot. Tidskr. 46(1):72, fig. 74-f, 1952.

? *Plagiochila oreocharis* Spruce, Trans. and Proc. Bot. Soc. Edinburgh 15:498, 1884-85; Herzog, Svensk Bot. Tidskr. 46(1):72, fig. 7a-d, 1952.
Plagiochila ludoviciana Sulliv., Musci Alleg. (Exsic.) No. 223, 1845; Sulliv. Amer. J. Sci. and Arts II, 1:73, 1846; Evans, Bot. Gaz. 21:192, pl. 16, figs. 4-12, 1896, in part.
Plagiochila patula var. *b leiboldii* Gottsche, Mex. Leverm. 105, pl. 2, 1863.
Plagiochila aliena Gottsche, Mex. Leverm. 118, pl. 1, 1863.
Plagiochila schliemiana Gottsche, Mex. Leverm. 123, pl. 1, 1863 (at least as to var. *b*).
Plagiochila schiedeana Gottsche, Mex. Leverm. 149, pl. 9, 1863.
Plagiochila subcristata Gottsche, Mex. Leverm. 150, pl. 10, 1863.
Plagiochila plicata Lindenb. et Gottsche, *in* Nees, Gottsche et Lindenb., Syn. Hep. 644, 1847?; Gottsche, Mex. Leverm. 152, pl. 9, 1863.
Plagiochila punctualis Gottsche, Mex. Leverm. 153, pl. 10, 1863.
Plagiochila tunarum Stephani, Spec. Hep. 2:189, 1906 (Cuba, *Wright*).
Plagiochila undulifolia Herzog, Hedwigia 72:219, fig. 11, a-f, 1932 ?

Plants robust, usually in loose patches or dense mats, dull to deep green to yellowish or olive-green, but never strongly brownish, dull, showing strong differentiation into a creeping rhizomatous stem-system and sharply ascending aerial leafy stems that stand away at an angle from the (usually vertical) substrate. *Mature aerial shoots* 2.5-4.2 (4.7) *mm wide,* infrequently furcate or *pseudodichotomous* (but frequently with 1 or often with 2 elongate innovations below the female inflorescences), rarely with solitary monopodial branches. Stems *ca.* 200-235 μ, occasionally 260-310 μ in diameter, the cortical cells strongly thick-walled, somewhat brownish, in 2-3 (4) layers, slightly smaller in diameter than the thin-walled medullary cells; medullary cells in at least 8 layers. Rhizoids on aerial shoots absent or virtually so. Leaves always *strongly imbricate, widely and nearly horizontally spreading* when moist *in a nearly flat plane,* at an angle of 75-85° (95°) with stem-apex; *postical margin usually at an angle of* 90-100° (rarely 110°) *with stem-apex; leaves narrowly obliquely ovate to ovate-falcate,* varying from 0.95-1 mm wide x 1.25-1.35 mm long to 0.97-1.1 mm wide x 1500 μ long (*type!*) to 750 μ wide x 1650 μ long to a maximum of 1500 μ wide x 2500 μ long (the *leaf-length ca.* (1.35) 1.45-1.7 × *as long as its subbasal width*); leaves with insertion exceedingly elongate (*the line of insertion ca.* 0.85-1.1 × the leaf-width), the dorsal base exceedingly long-decurrent; antical margin suberect basally (40-45° with stem), gradually arching outward and concave, the distal half of the antical margin eventually widely spreading ([75] 85-100° with stem), ventral (anterior) margin *strongly arched and dilated above the base, but virtually straight on distal two-thirds of leaf;* leaf apex usually narrowly truncate or rounded-truncate, sometimes subacute; *postical base long-decurrent* (*decurrent strip broad, standing stiffly away from the postical-stem surface to form a crista, but not strongly reflexed to form a postical pocket*), the decurrent portion wide, extending typically for 0.4-0.7 the merophyte length; *decurrent strip edentate;* postical margin above base usually with 5-10 more or less spinose marginal teeth; leaf-apex with generally 3-5 spin-

Fig. 64.—*Plagiochila ludoviciana* Sulliv. 1. Shoot with juvenile perianth, propagulum-free (x 16.5); 2-3. Female bracts (x 16.5); 4-5. Leaves (x 16.5); 6. Shoot-sector, postical aspect (x 16.5); 7. Juvenile perianth (x 16.5); 8. Cilia of perianth-mouth (x 182); 9. Cells of base, along decurrent strip (x 182); 10. Cells of leaf-base, along midline of leaf (x 182); 11. Cells of leaf-apex (x 182). (All from *Schuster* 22975, Van Cleave, Miss.; figs. 2-7 drawn to bottom portion of scale; figs. 8-11 drawn to top portion of scale.)

ose apical teeth; distal one-third of antical margin often with 1-3 spinose teeth (the marginal teeth of the entire leaf varying from *ca.* 9 to a maximum of 16 [*type*], rarely, in mod. *spinosissima* up to 22-26); cnemis strongly developed, the median leaf-base medially strongly longitudinally sulcate for 1/3-1/2 the leaf-length, together with the strongly reflexed antical margin resulting in an elongate, often falcate, arched convex dorsal fold extending for 0.4-0.6 the leaf-length. Apical and subapical cells (14) 16-18 x 18-23 μ to 20 x 20 μ; median leaf-cells 18-23 μ wide x 25-32 μ, the walls slightly or not thick-walled, except for the marginal 1-several cell-rows, *which usually have* $\pm$ *thickened tangential walls,* elsewhere the *trigones normally coarse and bulging,* occasionally confluent; cells at middle of leaf-base averaging 1.5-2 times as long as wide, from 20-21 x 30-40 (44) μ to 24-26 x 32-40 μ, with coarse, often $\pm$ confluent trigones. Cells of the decurrent postical base variable, usually *with longitudinal walls strongly thickened,* nearly evenly so, the cells becoming narrowly rectangulate (length-width 3-4:1) and then 12-13 (15) x (30) 36-43 (55) μ. Oil-bodies usually 4-9 per cell, *distinctly segmented,* varying from very coarsely, few-segmented (segments to 3.5 μ) to more finely segmented (segments *ca.* 1-2 μ), the individual segments always protuberant; segments usually in 1-3 rows (on superficial examination); oil-bodies mostly ovoid to linear-ellipsoid or baciliform, 3-4 x 6-7.5 μ, a few to 3-4 x 9-10 μ; chloroplasts 3.5-4.5 μ. Underleaves *always distinct,* but usually difficult to see, often largely hidden, varying from vestigial (and then of 2-several laciniae or cilia) to *plurilaciniate, occasionally of 2-several acuminate segments,* to 700-1000 μ long, usually with several weaker subbasal cilia. Asexual reproduction almost universally present (even on the perichaetial bracts), *by means of leafy propagula* from the postical (more rarely to some degree also antical) leaf-surface, the propagula deciduous with age; the *leaves persistent.*

Female inflorescence terminal, most often with one, occasionally two elongating innovations from beneath the lower half of the leaf-axil(s); perichaetial bracts similar to leaves, less decurrent, 1.6-1.85 mm long x 1100-1250 μ wide (or larger; measurement based on plant with leaves only 1.2-1.5 mm long), similar to leaves, but with postical margin relatively strongly undulate-crispate, bearing 22-26 or 32-40 sharply spinose, rather *irregularly sized teeth;* teeth largely confined to postical margin and apex of bracts, but 2-5 (occasionally 5-8) on the distal 0.5-0.7 of the convolute antical margin, more rarely the antical margin nearly as copiously dentate as the postical margin; base strongly concave and sheathing the terete basal portion of perianth. Perianth strongly laterally compressed above, but nearly terete near base with a long dorsal keel (length to mouth *ca.* 1.75-2 mm dorsally), but usually a very short postical keel (length *ca.* 0.4-0.5 the dorsal keel); *dorsal keel not or narrowly winged,* the wing entire; postical keel unwinged; mouth very wide, partly as a consequence of the $\pm$ oblique truncation, the width of the mouth often equal to or greater than length of dorsal keel; only dorsal portion of perianth inflated, but the broad postical portion strongly compressed down to perianth-

base, forming a broad flat "wing" that is often reflexed; perianth-mouth ± densely, strongly spinose-ciliate, the cilia uniseriate nearly to base, to 10-12 cells long, close; cells of cilia *ca.* 18 μ long x 13-15 μ wide.

Type.—Louisiana (*Sullivant,* Musci Alleghaniensis Exsic. No. 223, 1845). (Figs. 63:2-3, 6-9; 66:1-4.)

Distribution.—A very common and polymorphous neotropical species, whose range to our south is still very imperfectly understood, since presumed variants of it have been described as discrete species (particularly by Gottsche, Stephani and Herzog), from Mexico southward to Bolivia. The problem of the neotropical range of *P. ludoviciana* is difficult to solve, since the descriptions (and, if given, the illustrations) of closely allied taxa are often meaningless or nearly so.

Detailed, exhaustive studies of the variation of North American material of *P. ludoviciana* have demonstrated a very great polymorphism in this species. This polymorphism is partially the consequence of the varied environmental conditions the species occurs under, but is evidently also in part genetic in nature. It seems impossible to link the individual modes of variation (of the individual characters) into any pattern. Consequently, the species is broadly delimited here. The variability is discussed in detail, *vis-a-vis* that of *P. miradorensis* on pp. 71-85.

The excellent illustrations of Gottsche (1863) indicate that as many as six, possibly seven, taxa recognized for Mexico in this complex are inseparable from *P. ludoviciana.*

Under the name *P. plicata* Gottsche (1863) figures two forms (*a* and *b*). His fig. 7, of the form *a* suggests a long-decurrent postical leaf-base. In this case, the plant would fall in the *P. ludoviciana* complex. However, some of the other figures given (particularly of the var. *b*) suggest a short-decurrent form, similar to *P. hypnoides, P. serrata* and their relatives, to which Gottsche also compares them. Similarly Gottsche's *P. patula* var. *leiboldii* appears quite inseparable from forms of *P. ludoviciana.* However, it is very questionable whether it has anything to do with *P. patula* s. str. The latter was described from Jamaica (Swartz, Fl. Ind. Occ. III:1844, 1806); Lindenberg (Spec. Hep. Fasc. I:pl. 3) illustrates it as with a notable short-decurrent postical base. If this illustration is correct, *P. patula* is quite distinct from *P. ludoviciana* s. lat. In contrast, *P. patula* var. *leiboldii* has a leaf-form, dentition of the leaves, and long-decurrent cristate leaf-base closely matching many forms of *P. ludoviciana.*

Unfortunately, with the destruction of the Gottsche collections at Berlin, the synonymy cannot be determined at this date with any absolute certainty. Where possible doubt exists, the Gottsche species have been indicated in synonymy by a question mark.

Material from Panama has been seen (NYBG), sub *"P crispula* Lindb." (leg. W. Seeman), which appears inseparable from *P. ludoviciana.*

It is possible that *P. ludoviciana* Sulliv. is conspecific, although certainly not totally identical, with *P. guilleminiana* Mont., a very widespread neotropical species ranging from Ecuador to Bolivia, possibly to Brazil and Paraguay (see Herzog, 1952, p. 75) and to Nova Granada. Since reduction to synonymy of *P. ludoviciana* under the

earlier *P. guilleminiana* must involve comparison of the type plants, and since the type of the latter species is not available to me at present, it appears unwise to "sink" *P. ludoviciana* at present. Nevertheless, *P. ludoviciana* shares in common with *P. guilleminiana* a long and impressive series of suggestive features, among them: (1) leaves ovate-triangular, with both antical and postical bases long-decurrent (compare Herzog's [1952] Fig. 6a, of the type of *P. guilleminiana* with my Fig. 66:1, the type of *P. ludoviciana*); (2) the dentition of the leaves most marked distally, the area above the decurrent base, and the margin along the decurrent base, essentially or quite edentate; (3) perianth generally without a toothed antical keel, the antical keel either weakly carinate, or (at least on juvenile perianths) sometimes ecarinate (compare Herzog's Figs. 5f, 9c, with my Figs. 61:1-2; 64:1, 7); only rarely is the antical perianth keel well-marked and then may end abruptly in a blunt to acute tooth (compare Herzog's Fig. 8d with my Fig. 65:3); (4) the female bracts are, in both instances, much more strongly ciliate-dentate to spinose-dentate, as compared with the ordinary vegetative leaves (compare Herzog's Figs. 5a and e, 8c, and 9b with my Figs. 64:1-3, 65:9-10), and "tend" to exhibit identical variations in shape; (5) the underleaves are in both cases divided into several primary laciniate divisions; in both cases they may be rudimentary (see discussion on p. 91. Herzog (*loc. cit.*, p. 74) describes those of the type of *P. guilleminiana* as "meist ganz rudimentär and unscheinbar," but states that with respect to the degree of development of the underleaves there are recognizable "recht wechselnde Verhältnisse. . . Schon an dem Montagne'schen Original lassen sich die hier allerdings rudimentären Amphigastrien nachsweisen und gleiches gilt von den meisten brasilischen Belegen . . . wie auch für die uns vorliegenden ecuadorischen Pflanzen." Herzog emphasizes that the underleaves are mostly in the form of "winzigen, unregelmässig zerschlitzten Gebilde" and states that they are absent on branches and are not uniformly demonstrable even on the main stems. Although the large majority of collections of typical *P. ludoviciana* possess conspicuous and plurilaciniate underleaves, the underleaves may be small and difficult to demonstrate in some of the plants from our area, *e.g.*, in *Schuster* 22986, 22987 (Fig. 66:17), and in *Schuster* 22975 (Fig. 64:6); even in the type (Fig. 63:2, 9) the underleaves may be locally rudimentary, although usually readily demonstrated. In those plants (*e.g. Schuster* 22986) where the underleaves are reduced to two or three minute, filiform vestiges to 500-600 μ long, the other characters of the species are strongly deviant. It is possible that taxonomic segregation of these variants will prove necessary. Herzog (*loc. cit.*, p. 75, Fig. 12a-b) emphasizes that in some Ecuadoran phases of *P. guilleminiana,* which he segregates as a var. *grandistipula,* the underleaves may be of "ungewöhnlicher Grösse und mannigfaltiger Gestalt."

I have examined a perianth-bearing specimen assigned to this form by Dr. Herzog (Ecuador: Prov. Santiago-Zamora, Patuca, 600 m., *Karling* 2287! *leg.* Herzog). The underleaves here are usually vestigial, and the term "*gran-*

distipula" appears unwarranted, at least by comparison to the "normal" condition in *P. ludoviciana.* These plants, which have the dentition of the leaves and bracts very closely similar to that of typical *P. ludoviciana,* hence coarser than normal for *P. guilleminiana,* diverge from *P. ludoviciana* in one other respect, aside from the reduced underleaves: the perianths are very sharply and often widely winged dorsally, the wing often complete and bearing several teeth above. (This is, apparently, never the case in our *P. ludoviciana.*) Inversely, a specimen from the Herzog herbarium (Brazil: Paso Alegra, *Hoehne,* 1927) labelled simply *P. guilleminiana,* which is very similar in leaf form, size and dentition to the preceding one cited, has much more readily discernible underleaves. Although these are shorter than in *P. ludoviciana* (usually 200-500 μ long), they are similarly divided to near the base into 2-4 major laciniform lobes that range from 4-8 cells broad at base; these lobes are short and soon resolved into several short cilia, each normally ending in a slime papilla. Similar underleaves occur frequently in "*P. guilleminiana* var. *spinosissima* Herz." in a Bolivian plant (Tolopolo near Coroiro, 1300 m., *Buchtien,* 1912). The underleaves, in both of these plants, in view of the optimal size of the plants as a whole, are still much smaller than in *P. ludoviciana.* More normal is the condition in Brazilian plants (Morro de Taragua, S. Paulo, *Hoehne,* 1921), in which the underleaves are vestigial and consist of several minute, filiform laciniae only 2-3 cells wide at base.

Thus, from an examination of a series of specimens of various phases of *P. guilleminiana,* as well as of the type material of the presumed synonyms, *P. oreocharis* and *P. rhizophila,* there emerges a definite impression that the ventral merophytes in these plants are greatly reduced and the underleaves in general very small. Even in plants where they are distinct they are very short and fail to attain a length over 0.3-0.4 the maximal leaf width.

This contrasts strongly with the "normal" condition in *P. ludoviciana,* in which the normal phases have underleaves 0.5-0.9 the leaf width, see *e.g.,* Figs. 61:8, 63:12, 65:5-7, 15-16, 66:8 and 68:22. As a consequence we must conclude that there exists in both the South American *P. guilleminiana* and the North American *P. ludoviciana* broad variation in underleaf form and size, suggesting a very immediate genetic relationship between the two, but the range of variation in the two taxa is clearly quite different. The two "species" also agree closely in the evident tendency for the perianths, whether juvenile or nearly mature, to have the mouth oblique and the postical keel abbreviated in length (compare Herzog's Fig. 8d and 9c with my Figs. 61:2, 64:7, 65:3-4). Such a comparison will also show that the wide differences in form of the cilia or laciniae of the perianth-mouth of *P. ludoviciana* easily suffice to encompass the apparently more limited variation, in this respect, of the forms of *P. guilleminiana.* Herzog speaks of *P. guilleminiana* as a "weitverbreitete neotropische Art" that "zeichnet sich durch eine ungewöhnliche Vielgestaltigkeit aus." Herzog emphasizes, in addition to the form of the perianth and bracts (which we have already seen to be closely similar to those of *P. ludoviciana*), the leaf form of *P. guilleminiana* as a diagnostic feature, stating that "durchgreifend als Artmerkmal scheint . . . nur der gewellt herablaufende, meist ganzrandige Ventralflügel der Stamblätter

zu sein." He admits for the species, as was already emphasized by Stephani, a wide variability in the size and number of the teeth of the leaves; a similar variability, of course, is one of the marked attributes of our *P. ludoviciana!* Although the type of *P. guilleminiana* (see Herzog, *loc. cit.*, Fig. 6a) is only sparingly provided with short, triangular teeth in the distal one-fourth of the leaf Herzog figures (Fig. 8) a fo. *spinosissima* with much sharper teeth, extending down along the postical leaf-margin to within one-fifth of the leaf-base. The nearly edentate type plant can be nearly matched in North American plants (compare Figs. 65: 1-2, 5-8 and 68:22); the mod. *spinosissima* of Herzog is a very close approximation, in dentition, to the type of *P. ludoviciana* (Figs. 63:2-3, 7-9, 67:1)!

Although a very close affinity of *P. ludoviciana* with *P. guilleminiana* is easily demonstrable, the nature of the relationship of *P. ludoviciana* to the South American *P. oreocharis* Spruce and *P. rhizophila Spruce* is open to question. I cannot, at the moment, express full satisfaction with Herzog's (1952) treatment of them, based on Stephani (1905), as simple synonyms of *P. guilleminiana* — and thus possibly conspecific with our *P. ludoviciana.* According to Herzog's figs. 7a and e, the postical leaf bases tend to be less developed and somewhat less decurrent, and the leaves "tend" to be broader in *P. oreocharis* than normal in the *P. guilleminiana-ludoviciana* complex. I, therefore, initially questionably placed these plants into synonymy under *P. guilleminiana.* Questionable also is the attempt to equate *P. oreocharis* with the *P. guilleminiana-ludoviciana* complex, on the basis of Herzog's figures. The former species appears to differ, as is clear from Herzog's figures, in both the armature of the perianth-mouth, and shape of the perichaetial bracts. The perianth appears armed in *P. oreocharis* with only some 13-14 long, spinose teeth on each side or lip of the mouth, according to Herzog's figure; in *P. guilleminiana* Herzog shows varyingly 22, 15 and 29 teeth; in *P. ludoviciana* there are 18-20 or 28-34 cilia or teeth per lip. Similarly, the female bract of *P. oreocharis* is shown by Herzog (fig. 7c) to be very broadly ampliate, while those of *P. guilleminiana* are shown to be more ovate (Figs. 5e, 8c, 9b) and agree more nearly with those I illustrate under *P. ludoviciana.*

However, careful study of the type plants of *P. oreocharis* shows the following divergences from Herzog's figures, and equally well, a marked similarity to *P. ludoviciana* in these features: (1) the leaves are very long-decurrent postically, to 0.7-0.85 or even 0.9 the merophyte length on mature shoot-sectors; this decurrent strip is even longer and more undulate than is normal in most forms of *P. ludoviciana;* (2) the leaf shape varies from broadly ovate-triangular to simply ovate-triangular, and agrees perfectly with the type of *P. ludoviciana*!; (3) the perianth-mouth is armed with 26-30 acuminate laciniae, similar to those shown by Herzog for *P. guilleminiana,* and similar to those I have drawn for *P. ludoviciana* var. *invisus*!; (4) the antical perianth keel is either lamellate and entire, or very broadly lamellate, with the upper end of the lamella ending in 4 close spinose teeth! On the basis of these observations there is nothing to keep these plants apart from *P. ludoviciana,* except that they possess rudimentary underleaves. (The single perianth found bearing teeth on the upper portions of the antical keel may be abnormal. At least such dentition is not usually present in species of this complex). One other point of divergence remains to be noted. In North American *P. ludoviciana* the female bracts usually have the deflexed antical margin entire or subentire, except near the

apex; in *P. oreocharis* the antical bract margins bear a number of spinose teeth or oblique spines. This tendency for more copious dentition of the female bracts is also present in *P. undulifolia* Herz., a plant which I would regard as probably conspecific with *P. ludoviciana.* Surely this feature, *per se,* is insufficient for maintaining these plants as separate species.

Part of the type collection of *P. rhizophila* (from Andes Quitenses: Rio Verde, Pastasa affl.) has been studied in the Yale herbarium. These plants, which are very robust, the shoots attaining a length of 5-6 cm and showing occasional dichotomies, agree habitually with *P. ludoviciana* and are identical in basic leaf-form and dimensions with the type of the latter. They show some variation in degree of decurrence of the postical leaf-base, in some cases it is decurrent for only 0.5 the merophyte length, in extreme cases for up to 0.65 the merophyte length. On this basis they agree with some forms of *P. ludoviciana,* and I would not hesitate to place the plant in synonymy under this were it not for one marked difference: the plants, although as robust as any form I have seen of *P. ludoviciana,* are provided with only vestigial and filiform underleaves. In my experience robust plants of *P. ludoviciana* almost always show perceptible underleaves. For that reason, I have doubts about these plants being conspecific with *P. ludoviciana,* although they cannot be separated specifically from *P. guilleminiana.*

The preceding observations of the types of Spruce's *P. oreocharis* and *P. rhizophila* thus run counter in some respects to the observations and figures of Herzog (*loc. cit.*). On the basis of my study of the types of these species, I can find only one marked difference between them and *P. ludoviciana,* namely the rudimentary underleaves. Spruce's two taxa are identical in this respect, differing from each other chiefly in the degree of postical decurrence of the leaves. In the minute underleaves they also agree with "normal" forms of *P. guilleminiana.*

I have also, independently, studied two plants in the Yale herbarium under the name "*P. guilleminiana.*" One plant, from Peru (Santa Anna, *H. W. Foote* 41) is virtually inseparable from the larger phases of *P. ludoviciana,* agreeing in the longly decurrent postical leaf-bases, which are even more undulate than those of our *P. ludoviciana,* and form elongated crests; these plants, furthermore, have distinct, if unusually small underleaves, divided into several ciliary divisions and/or laciniae. The latter are mostly 2, occasionally 3-4 cells wide basally. The other plant, from Bolivia (Prov. Cochabamba, near Incacorral, Jan. 1908, *Th. Herzog*) was determined by Stephani. This plant is extremely robust, but the leaves are more pellucid and lax, narrow and quite falcate, with the leaves narrower and more nearly pointed distally, and with a much abbreviated postical decurrence. They do not, in my estimate, agree with *P. guilleminiana* sensu Herzog (1952), nor with other plants seen referred to that species. These plants do not need to further enter the present discussion, since they prove only that Stephani's concept of *P. guilleminiana* was not sharp, suggesting his observation with regard to *P. rhizophila* and *oreocharis* may not be valid either.

The best, if only temporary, solution to these problems may be to tentatively retain Spruce's two taxa as varieties and to only tentatively

equate *P. guilleminiana* s. lat. with *P. ludoviciana* s. lat. Since the type specimen of the former has not been studied, any nomenclatural changes, especially the reduction of *P. ludoviciana* to synonymy, should remain in abeyance. This situation is rendered more complex by the fact that all of the South American collections in this complex which I have studied are uniformly free of propagula, and neither Herzog nor Stephani mention them for *P. guilleminiana*. This is possibly owing to the fact that the *P. guilleminiana* complex in South America is restricted to wet, deeply shaded forests ("Bergwald" in many cases), and hence the stimulus needed for propagulum-production (presumably strongly fluctuating moisture conditions and intermittent drought) do not obtain. The following key, then, must be regarded as a temporary attempt at a solution:

1. Underleaves usually well-developed, of several laciniae up to 4-10 cells wide at base, their length up to 0.2-0.5 that of lateral leaves; lateral leaves almost constantly with abundant propagulum-production (except in leptodermous shade extremes). .... *P. ludoviciana* s. str.
1. Underleaves usually vestigial and, if discernible, usually of cilia or laciniae usually only 2-3 (4-6) cells wide at base, less than 0.15 the leaf-length; leaves never producing propagula. (*P. guilleminiana* s. lat.) 2
   2. Leaves postically with the decurrence extending for 0.5-0.6 (0.65) the merophyte length. ....*P. guilleminiana* var. *rhizophila* (Spruce) comb. n.
   2. Leaves postically with the decurrent strip very long, gradually and acuminately narrowed, extending down for 0.7-0.85 (0.9) the merophyte length. ....*P. guilleminiana* var. *oreocharis* (Spruce) comb. n.

The type of *P. guilleminiana* should be checked against the preceding key in order to adjust the above nomenclature. Presumably it will be found to be identical with var. *oreocharis*, in which case the latter can be relegated to synonymy.

The writer has also had the privilege of studying the type of *P. undulifolia* Herz., through the kind cooperation of Dr. Th. Herzog. This species was based on material from Hacienda Simaco, on the road to Tipuani, Bolivia, *ca.* 1400 m (*Buchtien*). The plants are almost identical with typical *P. ludoviciana,* and differ from this merely in (a) reduced underleaves; (b) the leaves frequently with the teeth rather strong to within a short distance of the edentate basal one-fifth of the postical margin; (c) female bracts with the antical, recurved, margin spinose-dentate almost to the base. These differences do not warrant a distinct species. The first two of these differential features are relative characters, occasionally almost equally developed in *P. ludoviciana* from the southeastern United States. It is very doubtful if the more copious development of spinose teeth of the antical margin of the bracts necessitates recognition of *P. undulifolia* as a separate taxon. I would regard it as a form of *P. guilleminiana.* At best, one might conceivably justify recognition of it as a separate variety on the basis of the freely spinose-dentate antical margin of the female bracts.

In addition, a number of specimens have been seen that are referable to *P. ludoviciana* from Cuba: Sierra de las Yeguas, San Diego de los Banos, Prov. de Pinar del Rio (*Leon* 524!), male plants with unusually narrow leaves; no loc. data (Hepaticae Cubensis Wrightianae; type of *P. tunarum* Steph.!); no loc. data (Montagne herb., in NYBG). Inversely, the plants reported by

Evans (1911, 1918) as *P. ludoviciana* from the Bahamas and from the Virgin Islands all represent *P. hypnoides.* If true *P. ludoviciana* is dispersed through the West Indies, outside of Cuba, it is evidently rare there.

P. ludoviciana s. str. is distributed over the entire low-lying por-

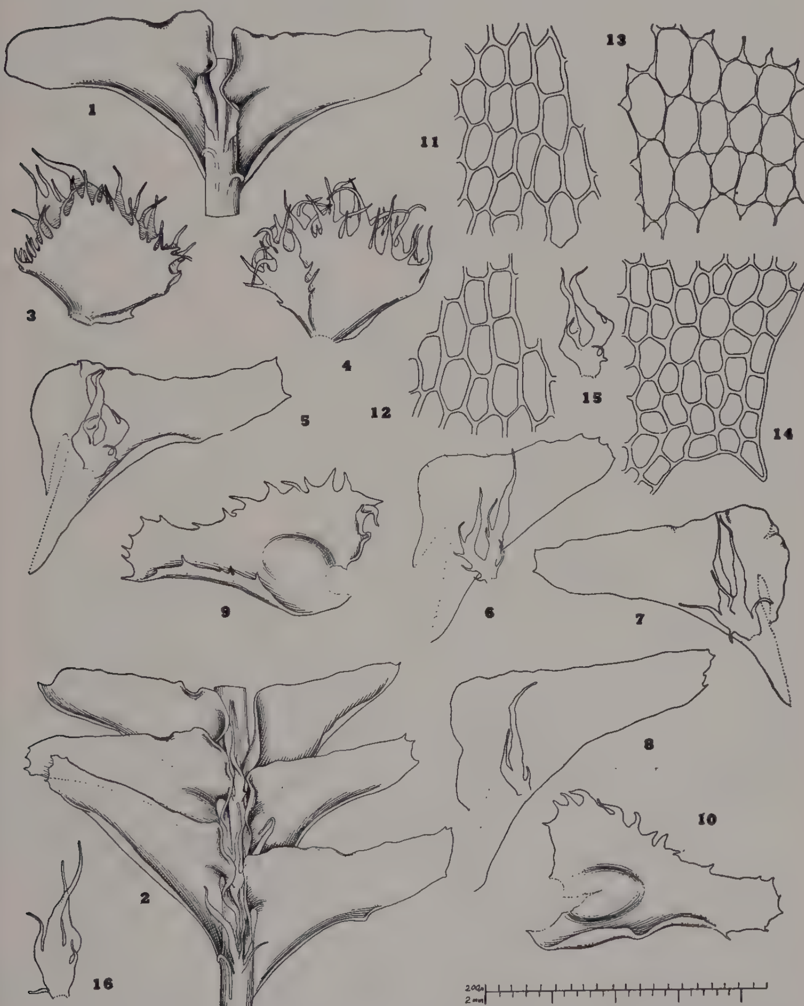

Fig. 65.—*Plagiochila ludoviciana* var. *invisus* Schuster. 1-2. Shoot-sectors, postical aspect (x 16.9); 3-4. Juvenile perianths, antical keels at right (x 16.9); 5-8. Leaves, with adjacent underleaves (x 16.9); 9-10. Female bracts (x 16.9); 11-12. Cells of postical, decurrent base (x 186); 13. Cells of base, along leaf midline (x 186); 14. Cells of leaf apex with tooth (x 186); 15-16. Underleaves (x 186). (All from type material from Pineola, Florida, *Sharp;* figs. 1-10 drawn to bottom portion of scale; 11-14, drawn to top portion of scale.)

tions of the Coastal Plain, from extreme coastal North Carolina southward to tropical Florida, westward along the Gulf of Mexico to eastern Texas; also in the West Indies. The species becomes relatively rare as the Piedmont is approached, but reappears at the edge of the Appalachian Plateau in Georgia, North Carolina, and South Carolina, being found as far inland as Tallulah Falls, Georgia (*Schuster* 34362) and in northwestern South Carolina, southwestern North Carolina, and southeastern Tennessee, where the species becomes localized and rare. Apparently lacking elsewhere in the old Appalachian Plateau region.

Numerous specimens have been seen in herbaria from the Appalachian system from Virginia to North Carolina and Tennessee. All of these have been found to be misdetermined, representing either *P. yokogurensis* subsp. *fragilifolia, P. virginica* or *P. virginica* var. *caroliniana.* The reports of this species from the Appalachians and Piedmont of these states (in Blomquist, 1936; Sharp, 1939; Patterson, 1950) must all be deleted.

NORTH CAROLINA: Near Wilmington, Brunswick Co. (*Patterson* 1420!); 3 mi. E. of Scuppernong, 30 ft., Washington Co. (*Anderson* 3983!; northernmost report); shale bluffs of Hiawassee R., Cherokee Co., 2000 ft. (*Anderson* 8077); also reported from six North Carolina counties by Blomquist (1936); all these reports referable to *P. yokogurensis fragilifolia* or *P. virginica.* TENNESSEE: Rabbit Creek, Lake Calderwood, Blount Co., 975 ft. (*Sharp* 3916!; the only previous correct Tennessee report!); Oconee R., above Reservoir, on Rte. 64, 3.4 mi. E. of jct. with Rte. 30, 14 mi. W. of Ducktown (*Schuster* 39513). SOUTH CAROLINA: Gorge of Estatoe R., N. Pickens Co. (*Schuster* 37676, 37669a); Charleston (*Fox,* 1918; *fide* Frye and Clark); Whitewater R. gorge, 0.2 mi. above bridge below Lower Falls, Oconee Co. (*Schuster* 40902, 40903). GEORGIA: Tallulah Falls, Rabun Co. (*Schuster* 34362, 34362a, 34377, 34380, 34380a); Thomasville, Thomas Co. (*Brown*!); Athens, 600 ft. (*R. M. Harper* 59b; *Harper,* June 26, 1900!; fo. with broad, entire-margined leaves); Coffee Co. (*R. M. Harper* 1448b!); no data (*Sullivant,* 1845!, NYBG). FLORIDA: Timm's Hammock, Dade Co. (*Small, Mosier* 52826, 5292, 5290a, 5282, *p.p.*); Hattie Bauer Hammock, Dade Co. (*Small and Mosier* 5297, *p.p.*, 5304, *p.p.*; both with androecia!); Nixon-Lewis Hammock, Dade Co. (*Small and Mosier* 5247, male!); Apalachicola R., Alum Bluff, Liberty Co. (*Schuster* 33537); dry coral limestone grottos at Pineola, Citrus Co. (*Schuster* 37229b, c. ♀, ♂ caps.; 37231, c per.; 37230a, narrow-leaved, xerophytic phase; c. per.; 37213, c. per., forma with largely erect-spreading leaves); Glen Julia, Gadsden Co. (*Schornherst* 2259!), Goodburn Hammock, Dade Co. (*Small and Mosier* 5233; plant superficially transitional to *P. hypnoides*); Snapper Creek Hammock, Dade Co. (*Small and Mosier* 6240!; the "*P. tunarum*" extreme); Sykes Hammock, Dade Co. (*Small, Mosier and Small* 5260!; the "*P. tunarum*" extreme); Ocala, Marion Co. (*Underwood* 1897 *pp.*, with *Euosmolejeunea clausa*); Lake City (*F. C. Straub* 107!); Snapper Hammock, Dade Co. (*E. G. Britton* 410, 501; "*P. tunarum*" extreme, ± leptodermous and shiny); Snapper Creek, S. of Coconut Grove (*Small and Nash* 465! c. per.; mod. *integrifolia-leptoderma,* near "*P. tunarum*"); Old Rhodes Key (*Small and Nash* 494; c. per.; mod. *integrifolia-leptoderma,* near "*P. tunarum*"); Royal Palm Hammock, Collier-Seminole S.P., Collier Co. (*Schuster* 20269, 26128, 26129, 26178a, 26125); 2 mi. SE. of Brooksville, Hernando

Co. (*Schuster* 22730a); Mathesson Hammock, on Old Cutler Rd., S. of Coral Gables, Dade Co. (*Schuster* 22689); Hillsborough State Park, Hillsborough Co. (*Schuster* 33905b, 33930b, 33901, p.p., among *P. aspleniformis, Lejeunea floridana;* 33905a, with *P. floridana, P. aspleniformis*). ALABAMA: Mobile (*Ch. Mohr*!); no loc. (Sullivant, Musci Allegh. No. 223, 1845; part of the type material from Alabama, part from Louisiana); near Chunchulla, Mobile Co. (*Schuster A*-109, *A*-144, *A*-155; c. perianth!; plate). MISSISSIPPI: 8-9 mi. N. of Escatawpa, on Rte. 63, Jackson Co. (*Schuster* 19184, 27833c); on Rte. 57, *ca.* 7 mi. S. of Ramsey Springs, N. Harrison Co., (*Schuster* 27785a, 27766b); 6-7 mi. NE. of Van Cleave, Jackson Co. (*Schuster* 22987, 27791, 22981, 22986, 19211b, 22975, 19242, 19241); Swampy woods, 2-3 mi. N. of Escatawpa, Jackson Co., (*Schuster* 27751a); Wyatt Hills, 15 mi. E. of Perkinston, George Co. (*Schuster* 20198, 27689a; Wyatt Hills, NE. of Ramsey Springs, W. George Co. (*Schuster* 27690a, 27710b, 20199, 26796a); Wyatt Hills, NE. of Ramsey Springs, George Co. (*Schuster* 26594c); Swamp along Black Creek, 7-8 mi. N. of Escatawpa, Jackson Co. (*Schuster* 29234, 29240a). ARKANSAS: Camp Albert Pike, Little Missouri R., N. of Langley, Ouachita Mts., Montgomery Co. (*Anderson* 11390a). LOUISIANA: no loc. data (Sullivant, Musci Allegh. No. 223, 1845, *the type;* in part from material from Alabama); no loc. data (Drummond, Musci Amer. No. 160! 1828, as *Jungermannia spinulosa*); Sulphur Springs near Covington (*Pennebaker,* July 2 1939!, as *P. ludoviciana;* includes almost entirely *P. dubia,* but 1-2 stems of *P. ludoviciana* admixed); Covington (*A. B. Langlois* 381!; admixed with *P. miradorensis*); Fricke's Cave near Folsom, St. Tammany Parish (*Mackaness B*-2, as *P. floridana*); 1 mi. W. of Robert, Tangipahoa Parish (*Correll* 9299, *p.p.,* among *Metzgeria myriapoda, Euosmolejeunea duriscula, Ceratolejeunea laete-fusca*).

Ecology.—Northward, *P. ludoviciana* is most frequently a species of the lower portions of tree-trunks (*Nyssa, Magnolia glauca, Persea, Fagus grandifolia*), usually occurring in the coastal *Magnolia-Persea* Evergreen forests, or in the old *Magnolia*-Beech forests. The species is confined to areas with low light intensity and high humidity (low evaporation rate). It occurs on bark usually up to a height of 4-5 ft. and often forms nearly pure mats near the bases of trees, or even on their exposed roots. The species in most of its area is usually not strictly pioneer in nature, but undergoes ecesis after invasion by the more mesic facies of the *Lejeunea-Radula-Porella* Associule. However, southward, in the tropical hammock forests of Florida, this species becomes ubiquitous and is found in a wider range of habitats. It occurs here on a wide variety of broad-leaved evergreen trees, as well as at the bases of *Taxodium,* the pond cypress. The phenomenal ability of the species to undergo ecesis here is undoubtedly correlated with the abundant production of leafy propagula, which are probably disseminated by raindrops (and possibly in part by gravity). Associated on the bark of trees, on such sites are a wide variety of other Hepaticae, chief among them: *Radula australis, Lejeunea laetevirens, Cheilolejeunea rigidula* and *opaca, Lopholejeunea sagreana, Metzgeria ciliigera* (more rarely *furcata* or *uncigera*), *Ceratolejeunea laete-fusca, Mastigolejeunea auriculata, Frullania squarrosa.* Less frequent associates are (in the area away from the tropical portions of Florida) *Radula*

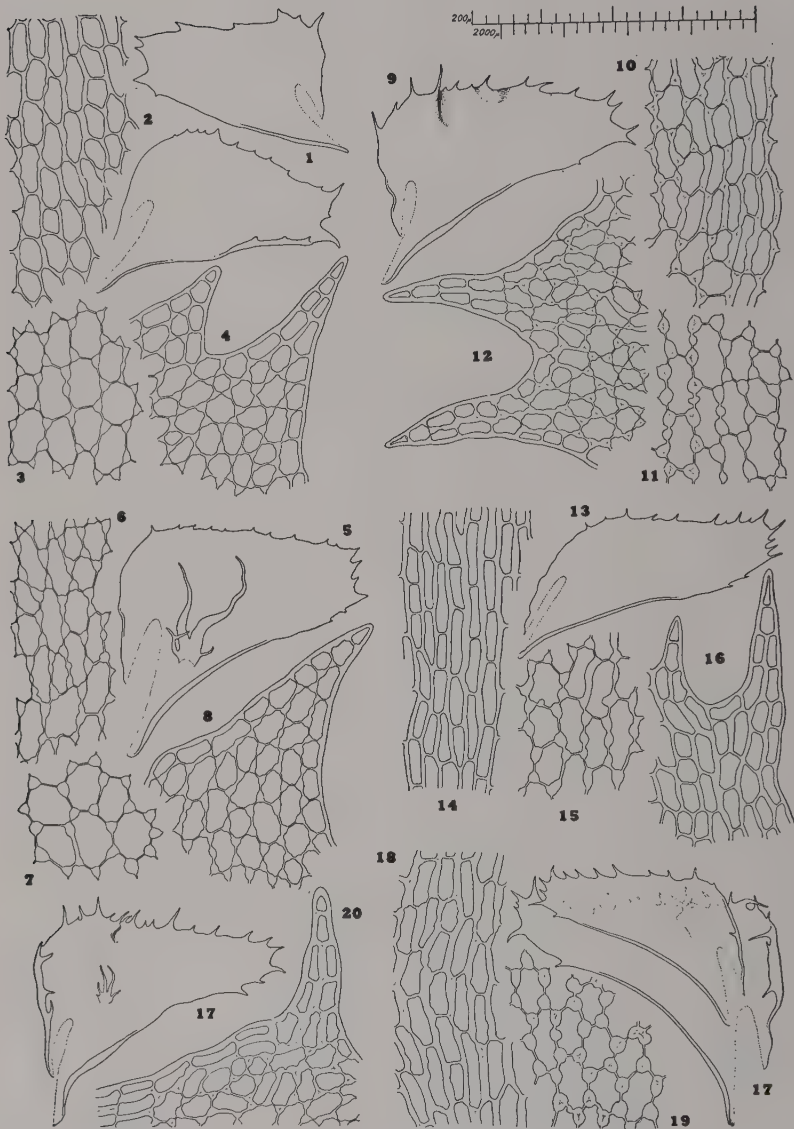

Fig. 66.—*Plagiochila ludoviciana* Sulliv. 1, 5, 9, 13, 17. Leaves and underleaves (x 16.5); 2, 6, 10, 14, 18. Cells of postical base, at origin of decurrent strip (x 182); 3, 7, 11, 15, 19. Median leaf cells (x 182); 4, 8, 12, 16, 20. Cells of leaf-apex (x 182). (Figs. 1-4 from type, leg. *Sullivant* [see also Fig. 63:2-3, 6-9, 11]; 5-8, Chunchulla, Ala., *Schuster* A109 [see also Fig. 61:1-3]; 9-12, N. of Escatawpa, Miss., *Schuster* 19184 [see also Fig. 63:1, 4-5,

obconica, andicola, and *caloosiensis, Neurolejeunea breutelii, Plagiochila undata, miradorensis, dubia* and *floridana, Rectolejeunea maxonii, Harpalejeunea ovata,* and lichens similar to *Chiodecton sanguineum.* In the deep tropical hammock forests of the southern tip of Florida frequently nearly confined to the bases of trees, forming large mats, associated usually with *Radula australis.* Such mats, of shiny, leptodermous plants, are scarcely typical; they represent an extreme form (described by Stephani as *P. tunarum*). In mats various ferns often undergo ecesis, chiefly *Campyloneurum phyllitidis.*

In subtropical and tropical Florida also occasional on shaded, moist banks, on coral limestone (as at Hillsborough R.), then with *Plagiochila aspleniformis* and *Lejeunea floridana.*

At the interior periphery of its range, the species is often saxicolous (as at Tallulah Falls, Georgia; near Murphy, North Carolina; and elsewhere), then occurring on damp to moist, shaded to intermittently sunny rocks in gorges, together with *Porella pinnata, Lejeunea laetevirens, Metzgeria furcata, M. myriopoda, Plagiochila undata, P. asplenioides,* occasionally *Scapania nemorosa* and *Frullania plana,* etc.; rarely *Radula andicola* and *R. voluta* are associated (Oconee R., Tenn.). In such areas the species appears to occur indiscriminately both on bark and on rocks, although more frequent on the latter. The populations from shaded rocks may be quite atypically slender, approaching *P. virginica* var. *caroliniana* in facies.

Differentiation.—*P. ludoviciana* has a distinctive appearance due to the following combination of characters: (1) large size (3-4.5 mm wide) and sparse dichotomous forking, except for innovations; (2) the rather narrow, asymmetrically ovate-triangular, tapering leaves, long-decurrent dorsally, tapering from the dilated base gradually to a narrow, often subtruncate apex that usually bears 3-4 teeth; (3) the nearly straight line formed by the postical margin, above the dilated postical base; the straight distal portion of the postical margin of mature leaves is furthermore normally at almost a right angle to the axis; (4) the virtually constant occurrence of propagula of the postical leaf-surface — usually in exceedingly great abundance; (5) the presence of large, usually bulging trigones; (6) the very dense leaves. These characters are shared, to a large extent, with the allied species, *P. hypnoides, P. miradorensis* and *P. undata.*

The plant, in nature, always occurs as a mod. *densifolia.* This results in a very characteristic appearance when examined ventrally — the dilated postical bases of the leaves are so closely crowded that the postical stem surface is virtually or completely hidden from superficial view (much as in the related *P. undata* and *P. hypnoides,* species which also occur only in the mod. *densifolia*). The postical leaf-bases are furthermore usually erect, often broadly reflexed, usually quite decurrent, and therefore form two approximated lines,

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of admixed *P. miradorensis*]; 13-16, *Schuster* 22986 and 17-20, *Schuster* 22987 [see also Fig. 62:1-3]; all leaf and underleaf figures drawn to bottom portion of scale; all cell figures drawn to top portion of scale.)

or crests, on the ventral stem surface. In material not typically developed, this feature is less apparent, and on branches, or on impoverished plants, the leaf-bases may be much as in the less derivative species, *P. hypnoides,* leading easily to confusion with the latter.

When robust and typically developed, easily separable from the somewhat similar *P. hypnoides* by the laciniate underleaves and by the longly decurrent postical leaf-base, which is usually erect (spreading away from the postical stem-surface at right angles). In this, *P. ludoviciana* exhibits affinities with *P. undata,* from which it differs at once in (1) the more or less coarsely dentate leaf-apex and postical leaf-margin (the teeth usually extending down near to the decurrent base on some leaves); (2) the sinuous or nearly plane, never strongly undulate postical leaf-margin of sterile plants; (3) the almost invariable occurrence of asexual reproduction through the development of brood plantlets from the lower leaf-surfaces (Fig. 64:4); (4) narrower leaves. At times the species occurs under atypical conditions, or in juvenile forms, which are difficult to recognize. Such forms may have the postical leaf-base less decurrent, and not or only narrowly reflexed (Fig. 62:10). Such forms must be separated from *P. hypnoides* with extreme care.

Although *P. ludoviciana* is very similar in some respects to *P. hypnoides* and *P. undata* (and has been widely confused with these two taxa in American herbaria and literature), it has been even more universally confused with *P. miradorensis,* a species which is often fully as common in the outer Coastal Plain as is *P. ludoviciana.* The separation of the two species, is, however, usually easily affected (see the detailed discussion under *P. miradorensis*). *P. ludoviciana* can usually be separated from *P. miradorensis* on the basis of (a) absence of a postical, reflexed-convolute pocket at the base of the leaf; (b) absence of dentition of the basal fourth of the leaf; (c) tendency for the cells at and just above the postical, decurrent strip of the leaves to be strongly elongated and more or less thick-walled on their longitudinal walls; (d) the laciniate underleaves, with the major divisions, at least, a number of cells broad towards base; (e) the edentate dorsal keel of the perianth; (f) the much less elongated perichaetial bracts.

There is also danger of confusing the weak, relatively short-decurrent leaved juvenile extremes of *P. ludoviciana* with *P. virginica* and its var. *caroliniana* Schuster. The writer has seen a considerable number of collections of *P. virginica* var. *caroliniana* in herbaria, under the name of *P. ludoviciana.* However, the pattern of modification of the two taxa is very different. The latter does not produce brown modifications with yellowish confluent trigones, while the xeromorphic phases of the former are brown and extremely strongly collenchymatous-celled. Furthermore, mature shoots of *P. ludoviciana* can always be recognized by the much denser leaves, with the dilated postical bases so shingled that the postical face of the stem is quite hidden from view; in *P. v. caroliniana* the leaf-bases never obscure the stem from below, nor is there any development of a crista.

A characteristic feature of this species is the almost invariable, and abun-

dant, occurrence of asexual reproduction by means of the development of small plants from the lower leaf-surfaces (Fig. 64:4). This is well-indicated in the type material (Fig. 63:7), and occurs in nearly all collections I have examined, which are at all adequate. Although the same type of asexual reproduction occurs in a wide variety of our other *Plagiochila* species, reproduction by leafy propagula is either of more sporadic occurrence in these species, or, when widely present, occurs relatively sparsely on each leaf (and has therefore been overlooked in most of our species — no indication of its occurrence being reported in the majority of them).

Variation.—See discussion of the variation patterns in the *P. ludoviciana-miradorensis* complex, on p. 71. In addition to the pattern of modification portrayed in that connection, there appears to be a considerable amount of genetic variation; some of the "species" questionably placed in synonymy under *P. ludoviciana* probably represent tropical vicariads (see p. 89-94). In spite of the immense variability regionally, both in leaf-shape, dentition, size of the underleaves, form and dentition of the female bracts, and dentition of the perianth-mouth, it seems impractical to recognize formal varieties, among the southeastern populations of the species, with the sole following exception:

Plagiochila ludoviciana var. **invisus** var. n.[2]
Fig. 65

Plantae in medio facie inter *P. ludoviciana* et *P. miradorensis;* folia angusta, subfalcata, apicibus attenuatis, 1.8-2.0 × longis quam latis; margines foliorum vere edentatae; postia lamina decurrens foliorum cellularum vix elongatarum; amphigastria maxima, laciniato-ciliata. Typus: Pineola, Citrus Co., Florida (*A. J. Sharp,* Dec. 16, 1948).

Plants rather robust, pale green, 3.1-3.7 mm wide. Stems 230-300 μ wide. Leaves densely imbricate, *narrowly, subfalcately, ovate-triangular, the distal portions prominently drawn out* (much as in "normal" phases of *P. miradorensis*), up to 1000-1100 μ wide at the ampliate base x1825-2050 μ long (length usually 1.8-2.0 × width); antical margin weakly concavely arched, very prominently long-decurrent, entire-margined to the apex; postical margin *very strongly ampliate and dilated above the decurrent* base, the decurrent base rather broad, *erect and forming a crista or slightly* (*and obscurely*) *reflexed,* not forming a discrete water-sac or basal fold; *leaf-margins virtually edentate,* the region above postical base entire, the postical margin entire to somewhat sinuous, *the ± narrowly truncate apex bearing 1-3 low and obscure teeth.* Cells moderately collenchymatous, the walls tending also to be equally thickened; apical cells *ca.* 17-20 μ wide x 23-28 μ long, *tending to be nearly equally thick-walled, little elongated;* cells at median base thinner-walled and with sharper, more salient trigones (22) 24-26 μ wide x 33-42 (52) μ long; cells of, and just above, the decur-

[2] The varietal name *invisus* meaning hateful or detested, a reflection of the author's reaction to the discovery of this taxon, which occupies a puzzling and problematical intermediate position between *P. ludoviciana* and *P. miradorensis.*

rent postical strip *virtually equally thick-walled, but only moderately elongated, ca.* 18-22 (23) μ wide x 30-35 (38) μ long, averaging less than twice as long as wide. *Underleaves very large,* to 1000-1150 μ long, of 2 major, tortuous, lanceolate-acuminate divisions, armed with basal and subbasal lateral cilia.

Female bracts very strongly ampliate above postical base, strongly narrowed towards the narrow, subtruncate apex; ampliate postical margin *coarsely dentate* with broad based, often irregularly bent, variously directed, *acute but scarcely sharp teeth,* distal half of bract and its apex with a few smaller but sharper teeth; antical margin revolute to the apex, with usually 3-5 sharp but small teeth of the distal 0.5-0.75 of the margin. Perianth (juvenile) with mouth coarsely and longly laciniate-ciliate, some of the divisions 3-6 cells wide at base, or more; the longer antical keel with a narrow but sharp wing in the basal half, which may gradually become vestigial above or end in an obtuse to subacute tooth.

Type.—Pineola, Citrus Co., Florida; on bark of *Sapindus* (*A. J. Sharp,* Dec. 16, 1948). The type was determined as *P. undata* Sulliv. by Redfearn, and formed the basis for the report of this species from Citrus Co., Florida in Redfearn (1952). Plants connecting this variant to typical *P. ludoviciana* are those of *Schuster* 33901, from Hillsborough R. State Park, Florida.

Differentiation.—*P. ludoviciana invisus* is a plant occupying a disturbingly intermediate position between *P. ludoviciana* and *P. miradorensis.* On first glance, it gives the impression of an almost typical form of the latter species, agreeing with it in the following superficial features: (a) rather pale or whitish green color, with slight brownish tinge; (b) rather pellucid cells and leaves; (c) the falcate, long drawn out and slender leaves, narrowly truncate at the apex in most cases, with their margins almost edentate. Under the microscope several other similarities to *P. miradorensis* become apparent, which are equally important: (a) the cells at the base of the long-decurrent postical strip little elongated, not forming a zone of sharply elongated, strongly thick-walled cells; (b) dentition much reduced — virtually lacking on most leaves. The impression the plants give, particularly that derived from the leaf-shape and the subentire leaf-margins, is strongly suggestive of *P. miradorensis.* Yet it is wholly impossible to place this material under the latter species, since it shows these major deviant features: (a) the underleaves are large, laciniate-ciliate, with the major lobes 4-6 cells wide at base or more; (b) the postical leaf-base is elevated as a somewhat crisped and undulate crista, but never shows any marked tendency to be reflexed to form a water-sac; this base of the leaf is entire; (c) juvenile plants (and these are preponderant in the collection) show no trace of a water-sac, and show only a slight tendency towards formation of a crista; (d) the perianths lack distinct teeth of the antical keel.

In some of the preceding features *P. ludoviciana invisus* agrees with typical *P. ludoviciana,* particularly in the edentate antical perianth keel; the total lack of a revolute postical leaf-base (and consequent

lack of a water-sac); the laciniate-ciliate underleaves. On the other hand, *P. ludoviciana invisus* differs from typical *P. ludoviciana* in the (a) lack of cellular differentiation of the postical leaf-base; (b) in the virtually edentate leaves, although extreme shade forms of typical *P. ludoviciana* may have almost edentate leaves; these quite fail to develop the mature aspect which the fertile plants of *P. ludoviciana invisus* possess; they also have much more abbreviated leaves, not at all falcate in form; (c) in the falcate and drawn-out distal portions of the leaves; (d) in the lack of any marked tendency for the cells of the leaves to become prominently elongated at the leaf tips. These differences seem slight, yet cannot be reconciled with the broad pattern of variation exhibited by "normal" *P. ludoviciana.* It is particularly impossible to reconcile the facies of these plants, which is totally that of *P. miradorensis,* with the *P. ludoviciana*-like underleaves and form of the postical leaf-bases.

The type material has been confused with *P. undata.* Although the crispate basal portions of the postical margins of the leaves might suggest *P. undata,* no immediate relationship to that species is possible. The narrow, attenuated leaves are quite unlike those of *P. undata* (although their subentire margins suggest those of *P. undata*). *P. undata* differs further in the broadly winged and dentate antical keel of the perianth.

PLAGIOCHILA MIRADORENSIS Gottsche

Figs. 61:4, 5; 62:6-7; 63:1, 4-5, 10; 67:6-18; 68:1-21; 69; 70

Plagiochila cucullata var. *b* Gottsche, Lindenb. and Nees, Syn. Hep. 642, 1847.
Plagiochila miradorensis Gottsche, Mex. Leverm. 127. pl. 10, figs. 1-10, 1863.
Plagiochila ludoviciana Evans, Bot. Gaz. 21:192, 1896 (p.p; at least as to figs. Pl. 16, figs. 5-7, 12); Kurz and Little, Bull. Fla. State College for Women 24(3):34, fig. 48, 1933 (at least p. part); Frye and Clark, Univ. Wash. Publ. Biol. 6(3):454, figs. 2, 5-6, 8-9 (in part).

Plants in robust patches, pale green to somewhat olive green, the aerial shoots ascending, simple or sporadically pseudodichotomously furcate; shoots 2.8-3.8, occasionally to 4.75 mm wide, rather robust; stems 200-300 μ in diameter, commonly yellowish-brown, rather rigid. Leaves *closely imbricate, extremely polymorphous,* varying from narrowly *ovate-falcate to lanceolate-falcate* or even rectangulate-falcate, from a minimum of 1580 μ long x 840 μ wide to a median figure of *ca.* 1875-2100 μ long x (850) 900-1050 μ wide, occasionally to 2250-2450 μ long x 1075-1475 μ wide; *leaves with base erect and sheathing when dry (only the* $\pm$ *convolute and twisted distal, narrow "limb" strongly laterally spreading)*; when moist laterally spreading from *ca.* a 45-55° angle, at base, to a 90-100° angle in the distal half of the leaf; postical margin at usually *ca.* a 90-100° angle with stem; *postical margin ampliate above the long-decurrent base,* the distal two-thirds of the postical margin nearly straight or slightly falcately arched, subparallel to distal portion of antical margin, or gradually convergent to it; *postical base rather broadly dilated* (including the decurrent por-

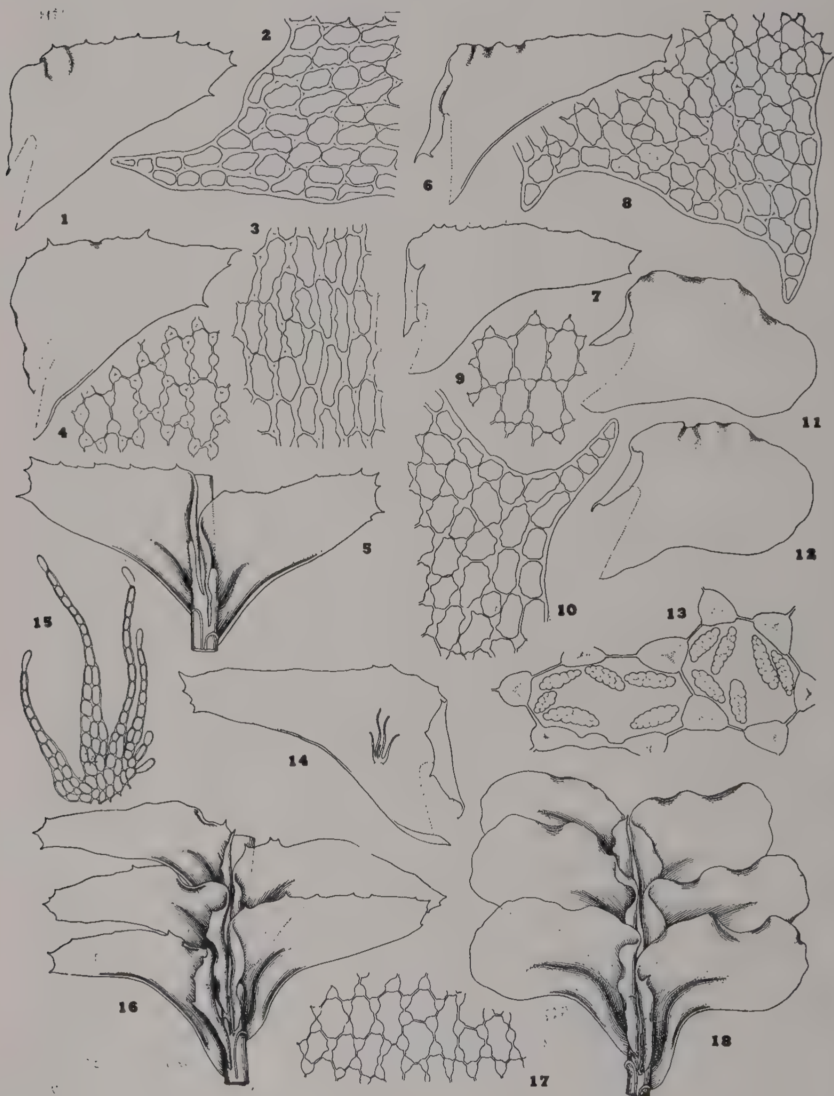

Fig. 67.—*Plagiochila ludoviciana* Sulliv. and *P. miradorensis* Gottsche, from plants growing admixed. 1-5. *P. ludoviciana.* 1. Leaves (x 16.5); 2. Cells of leaf-apex (x 182); 3. Cells of postical leaf base (x 182); 4. Cells from base of leaf near middle of leaf (x 182); 5. Shoot-sector, postical aspect (x 16.5). *P. miradorensis.* 6-7. Normal leaves (x 16.5); 8. Leaf-apex cells (x 182); 9. Cells of leaf base along midline (x 182); 10. Cells of leaf at and just above postical decurrent base (x 182); 11-12. Atypical leaves (x 16.5); 13. Median cells with oil-bodies (x 635); 14. Leaf and underleaf (x 16.5); 15. Underleaf

tion), *long-decurrent* (for usually 0.55-0.75 the merophyte length), the decurrent strip and basal portion above it *strongly reflexed-convolute, the free margin often* $\pm$ *involute* (and thus not exposed to view), forming a somewhat tubular water-sac; antical margin reflexed for usually the basal 0.5-0.7, normally somewhat arched, but in extremely narrow-leaved forms often almost straight. Leaf-margins variable, but the *teeth always less sharply developed, and fewer than in P. hypnoides, usually much less sharp* (*and often fewer*) *than in P. ludoviciana;* apex commonly obliquely truncate, the angles of the truncation marked by 2 low teeth, of which the lower may be obsolete (the leaf then merely obliquely acute at tip), more rarely both obsolete, and leaf then rounded at apex; postical margin, above the base, frequently *almost or quite edentate, occasionally with* 2-6 (8-12) *low and weak teeth* (1-3 cells long x 1-2 cells wide at base), the teeth never truly spinose, *broad-based and merely acute,* often reduced to angulations, *or the margin merely sinuate;* postical, reflexed base normally more *sharply and prominently spinose-dentate, or short-ciliate, bearing usually* 1-5 (6) *teeth* (1-several of which may be hidden and involute; occasionally with teeth only 0-1); antical margin edentate, except (rarely) for 1-2 preapical low teeth. Cells always *strongly collenchymatous*: the cells of the leaf-apex and upper leaf-margins *nearly isodiametric,* with coarse, nodular trigones, separated by sharply defined thin regions, the *trigones thus rarely if ever broadly confluent;* apical and subapical cells *ca.* 18-20 (23) μ x 20-25 (27-30) μ; median cells little elongate, with coarse, well-defined trigones, 18-23 x 26-30 (32-38) μ; basal median cells little elongated, with coarse, nodular trigones, occasional intermediate thickenings, 22-27 (32-35) x 30-35 (36-40) μ; cells of the postical, decurrent portion somewhat smaller, strongly collenchymatous (the trigones occasionally somewhat confluent, but *never to the point where the walls become subequally thickened*), *little or moderately elongated* (length: width 1-2, rarely 2.5-1), *ca.* (16) 18-24 x 24-33 μ. Oil-bodies segmented, as in *P. ludoviciana,* commonly 5-8 per cell, *ca.* 3-3.5 x 5-9 (11) μ, formed of (1) 2-3 rows of coarse, protuberant spherules or segments. *Underleaves slender and small, formed of 2-several linear, often tortuous cilia that are uniseriate for much or all of their length;* cilia occasionally branched, ending usually in clavate slime-papillae; total underleaf length to 500-975 μ. Asexual reproduction by propagula of the postical leaf-surfaces always present, usually less conspicuous and copious than in *P. ludoviciana.*

Dioecious. Mature perianth oblong-obovate, ca. 2.5 $\times$ as long as wide as at mouth, the antical keel narrowly but distinctly winged, the undulate-reflexed mouth freely, but not contiguously spinose-ciliate;

(x 64); 16. Normal shoot-sector from shoot of same plant in fig. 18 (x 16.5); 17. Median cells (x 182); 18. Atypical shoot-sector, postical view (x 16.5). (Figs. 1-12, 14-18 all from *Schuster* 19242, near Van Cleave, Miss.; 13, from Juniper Springs, Fla.; figs. 1, 5-7, 11-12, 14, 16, 18 all drawn to same scale as bottom scale in Fig. 66; figs. 2-4, 8-10, 17 all drawn to same scale as top scale in Fig. 66.)

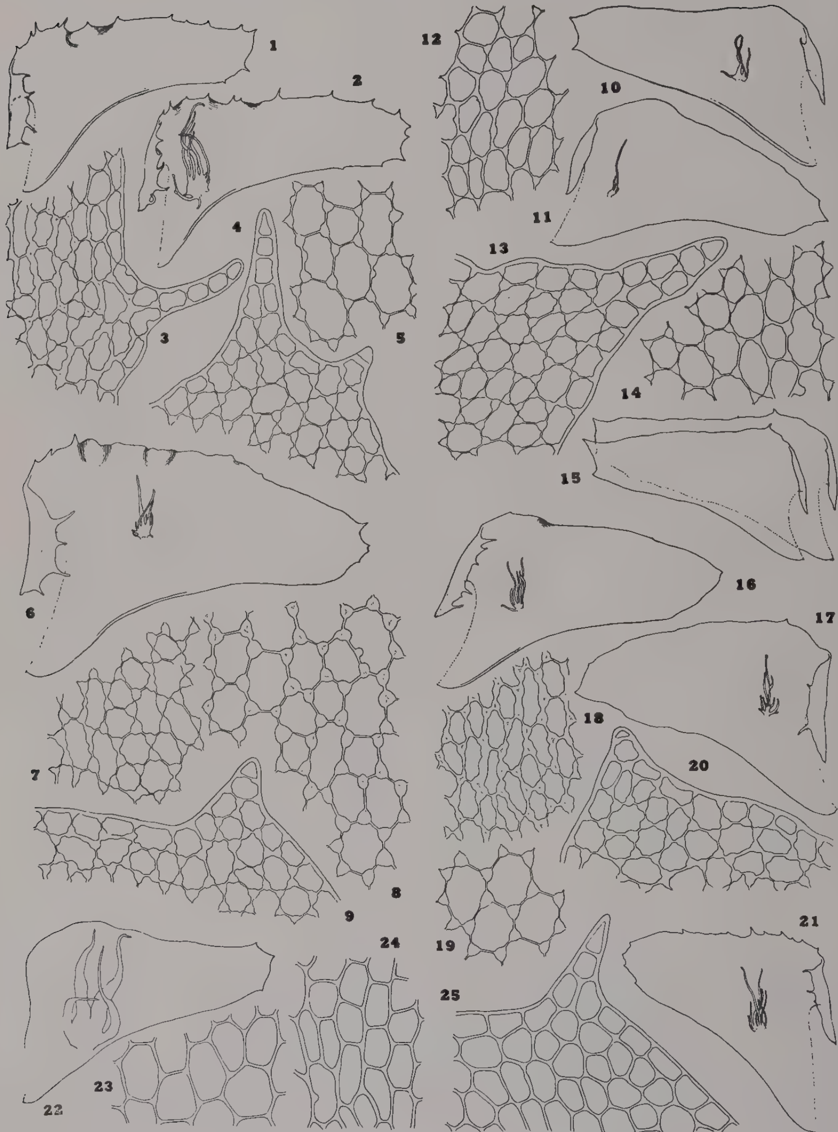

Fig. 68.—*Plagiochila miradorensis* Gottsche. (1-21) and *P. ludoviciana* (22-25). 1-2, 6, 10, 15-17, 21-22. Leaves and underleaves (x 16.5); 3, 7, 12, 18, 24. Cells of postical leaf-bases, just above decurrent strip (x 182); 4, 9, 13, 20, 25. Cells of leaf-apex, showing form of apical teeth (x 182); 5, 8, 14, 19, 23. Cells of leaf base, along midline of leaf (x 182). (Figs. of leaves and underleaves drawn to bottom scale in Fig. 66; figs. of cells all drawn to top scale in

antical wing 2-5 cells wide, extending from base to above middle (sometimes to apex) *bearing* 2-4 *sharp but small teeth;* perianth with the crispate-undulate and ± reflexed mouth quite oblique, the postical keel much shorter than antical. Capsule shortly exserted beyond perianth. Bracts as long as mature perianth, *ca.* 2.3-2.75 × as long as wide, sometimes dentate on the distal 4/5 of the antical margin (at other times with antical margin edentate) as well as on the entire postical margin and apex, narrowed to a subtruncate, narrow apex; bracts from 2400 μ long x 1050 μ wide subbasally (950 μ, with margin inrolled) to 2750 μ long x 1500 μ wide (1300 μ wide with antical margin rolled in), oblong-ovate and somewhat falcate, strongly narrowed distally (width near apex only 350-450 μ).

Type.—Near Mirador, Mexico (*ca.* 3000 ft.) (Liebmann). The type, in the Gottsche herbarium, presumably destroyed. *Neotype.*—Bogue Banks, Carteret Co., North Carolina (*E. Felton Jones* 2596) in herb. Duke University, and of author.

Distribution.—*P. miradorensis* appears to be distributed very much like the closely allied *P. ludoviciana,* but is much more strictly coastal in range, never occurring at the margin of the Blue Ridge or in the Piedmont. In our area confined to low elevations (below 300 ft., evidently), and occurring only in the outer Coastal Plain, although more widely distributed throughout most of central and northern Florida. To our south extending to Mexico, and very probably considerably farther southward. The range southward is almost impossible to ascertain at present, owing to the taxonomic confusion in this complex. In the United States extending from the Gulf Coast of Texas into Louisiana, Mississippi, Alabama, south to the Oligocene Island area of central (but not to southernmost!) Florida, northward along the Coastal Plain to slightly north of the Cape Hatteras region of North Carolina (where confined to the outermost edge of the Coastal Plain).

NORTH CAROLINA: Hoffman Forest, Bogue Banks, S. of Atlantic Beach, Carteret Co. (*Jones* 2596, neotype! mod. *latifolia-dentata*). GEORGIA: Okefenokee Swamp, Charlton Co. (*Blomquist* 11512!). FLORIDA: Hammock forest 3-4 mi. NW. of Brooksville, Hernando Co. (*Schuster* 22085a, 22110a, 22726a; mod. *angustifolia-dentata;* in part trans. ad var. *convoluta*); hammock forest N. of Gulf Hammock, Levy Co. (*Schuster F*-138, *F*-150; mod. *angustifolia-dentata,* and trans. ad mod. *latifolia-integrifolia*); Glen Julia, Gadsden Co. (*Schornherst* 2259, as *P. ludoviciana!* Most duplicates of this number, each containing only a few stems, are *P. miradorensis;* in one case some true *P. ludoviciana* (NYBG) was admixed); Juniper Springs, Ocala Ntl. Forest, Marion Co. (*Schuster* 31935); Sanford, Seminole Co. (*Rapp;* det. and reported as *P. ludoviciana* by Redfearn, 1953!; *Rapp,* May, 1918 and *Rapp* 31, as *P. ludovi-*

Fig. 66. Figs. 1-5, *Schuster* 22085a, Brooksville, Fla. [see also Fig. 61:4-5]; 6-9, *Jones* 2596, Bogue Banks, N.C. [see also Fig. 69:10-11]; 10-15, type of var. *convoluta* Schuster, *Schuster* 27759, Escatawpa, Miss. [see also Fig. 69:1-9]; 16-21, *Whitehouse* 23318, Texas [see also Fig. 62:6-7]; 22-25, *Schuster* 33901, Hillsborough R., Fla.)

ciana!); DeLeon Springs, Seminole Co. (*Rapp* 14!; as *P. undata,* Y); below Bartow, Polk Co. (*Vanning and Row* 154!); Ocala (*Underwood,* 1837, 1866, as *P. ludoviciana*!); Monticello (*Lighthipe* 26!, as *P. ludoviciana*); Rosewood (*A. P. Garber* 169, as *P. ludoviciana!*); Johnson's Juniper Swamp, 8 mi. S. of Bristol (*Kurz* 40!; with immature perianths); Gainesville, Alachua Co. (*N. L. T. Nelson* 106!). The last two collections served, in part, as the report of "*P. ludoviciana*" from northern Florida (in Kurz and Little, 1933). MISSISSIPPI: Swamp forest 2-3 mi. N. of Escatawpa, Jackson Co. (*Schuster* 19124a, 19250b, 1951; *Schuster* 27759, 1953, the var. *convoluta!*); near Pascagoula R., 6-8 mi. NE. of Van Cleave, Jackson Co. (*Schuster* 19242a p.p., 19213b, 19230e, 22981, p.p. with *ludoviciana*); swamp forest on Rte. 57, NE. corner of Harrison Co. (*Schuster* 2770b); Black Creek, 7-8 mi. N. of Escatawpa, Jackson Co. (*Schuster* 19184a, p.p., with *P. ludoviciana*). (These collections all the mod. *angustifolia-dentata,* but *Schuster* 27759 the var. *convoluta,* and *Schuster* 22981 trans. ad mod. *latifolia-integrifolia*); Biloxi (*Lloyd and Tracy, Sept. 1900!,* as *P. ludoviciana*); Bay St. Louis (*Langlois, Apr. 28, 1885!* as *P. ludoviciana*). LOUISIANA: Fricke's Cave near Folsom, in Magnolia bog (*Mackaness* B-4!, as *P. ludoviciana*); Lafayette (*Langlois* 5151!, 625! as *P. ludoviciana*); Bayue Station (*Langlois* 516!, as *P. ludoviciana*); Chinchuba, Tammany Parish (*Langlois* 620! as *P. ludoviciana*); near Duchamps (*Langlois* 624! as *P. ludoviciana,* Y); Chinchuba, at foot of trees in ravines (*Langlois, Apr. 20, 1891!*). TEXAS: Along creek, 7 mi. S. of Silsbee, Hardin Co. (*Whitehouse* 23318, 24988; mod. *latifolia-integrifolia* and transition to *latifolia-dentata*).

Ecology.—Usually somewhat xerophytic, occurring on dry bark, but also often in rather deep coastal swamp forests, under conditions of persistently high humidity. In our area often on the bases of trees along the slow-moving, sluggish, "black water" creeks along the immediate coast, in forests consisting of *Taxodium,* and the evergreen *Chamaecyparis, Magnolia virginiana, Persea borbonia, Cyrilla racemosa* and *Cliftonia monophylla,* and a few deciduous trees (*Acer rubrum; Nyssa sylvatica biflora*); it has been collected on the bark of the latter two trees. Here it may form large patches, amidst which the rhizomes of the fern, *Polypodium polypodioides michauxiana* grow, as well as the roots of the orchid, *Epidendrum conopseum.* Associated hepaticae, under such conditions, are *Mastigolejeunea auriculata, Cheilolejeunea rigidula* and *clausa, Ceratolejeunea laete-fusca, Radula caloosiensis, R. australis, Lejeunea flava* and *laetevirens, Metzgeria furcata* and *uncigera, Rectolejeunea maxonii,* more rarely *Cololejeunea contractiloba* (which may be ephiphytic on the *Plagiochila*), *Neurolejeunea breutelii,* and *Plagiochila ludoviciana.* The intimate admixture of the latter species (in *Schuster* 19184a and 19242a) is significant in affording us some means of measuring the degree to which these two allied species differ from each other.

The plant also occurs in mixed swamp forests (*Magnolia grandiflora-Ilex opaca-Quercus nigra*), where it has been found on the bark of the *Magnolia,* and on *Liriodendron* and *Quercus nigra,* associated with most of the Hepaticae previously listed. Associated there also with *Plagiochila ludoviciana* (in *Schuster* 22981; on *Q. nigra*). Occasionally also in rich, mixed, subtropical "hammock" forests, on the

bark of a variety of trees. In drier situations, as in partial sun, sometimes admixed with *Frullania squarrosa*. Inversely, occasionally on bark along streams, when mixed with *Porella pinnata*.

Differentiation.—*P. miradorensis* is allied most directly, among our species, to *P. ludoviciana*. It has been consistently confused with this

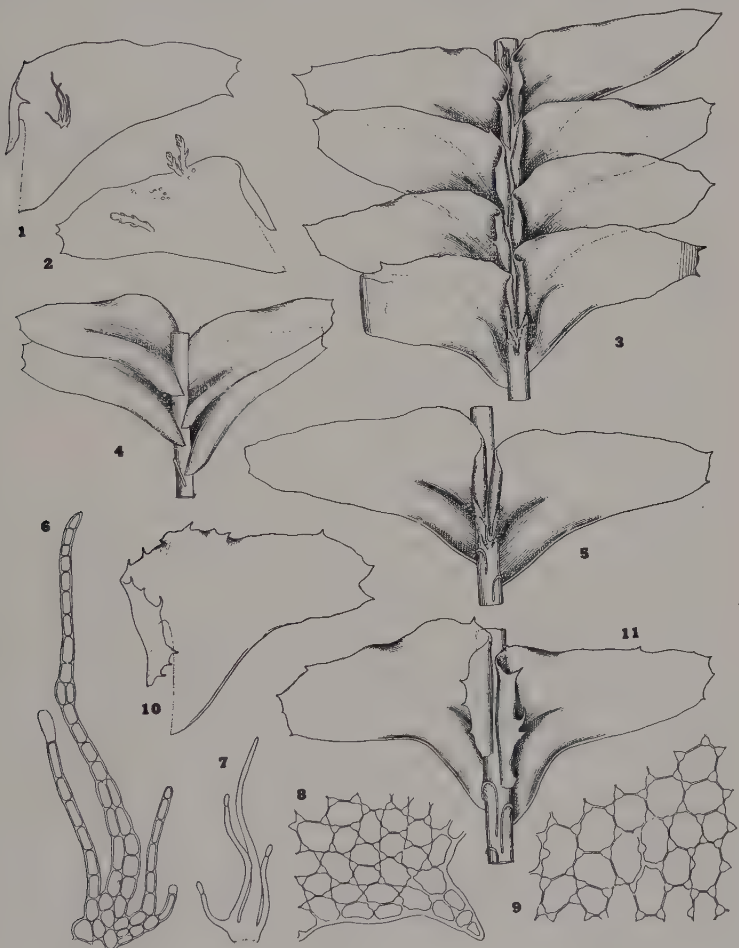

Fig. 69.—*Plagiochila miradorensis* var. *convoluta* Schuster (1-9) and *P. miradorensis* Gottsche (10-11). 1-2. Leaves and underleaf (x 16.5); 3, 5. Shoot-sectors, postical aspect (x 16.5); 4. Shoot-sector, antical aspect (x 11.7); 6. Underleaf (x 57); 7. Underleaf (x 29); 8. Cells near postical leaf base (x 180); 9. Cells near median base of leaf (x 180); 10. Leaf (x 12.4); 11. Shoot-sector, postical aspect (x 12.4). (Figs. 1-9, from type of var. *convoluta* *Schuster* 27759, Miss.; 10-11, from *Jones* 2569, Bogue Banks, N.C.)

species in all the American literature, starting with Evans (1896), going up to Frye and Clark (1944). For example, part of the cited material in Frye and Clark (*loc. cit.*, p. 454) is true *P. ludoviciana* as are their figures (1, 3-4) of the underleaves, whereas, a part of the cited material represents *P. miradorensis,* while the Virginia plant represents *P. yokogurensis.* The confusion between the two species is based largely on the fact that *both P. ludoviciana* and *P. miradorensis* are exceptionally variable species. Indeed, the variability of each is so great and the ability to produce parallel forms so marked, that I was, for a long time, willing to regard *P. miradorensis* as a synonym or variety of *P. ludoviciana.* The final proof that two distinct species were at hand came with the study of one collection (Van Cleave, Miss., *Schuster* 19242) in which both species were intimately admixed (Fig. 67:1-12, 14-18). In essence, therefore, the two taxa were available for study, *as grown under identical environmental conditions.* Both species were almost equally robust, and similar in color (although the plants of *P. ludoviciana,* as is apparently uniformly the case, were somewhat more chlorophyllose, consequently more opaque). Except for the few *P. undata*-like (abnormal?) extremes produced by *P. miradorensis,* both taxa were represented by "normal" phases (compare Fig. 67:5 and 16). Typical *P. ludoviciana* and typical *P. miradorensis,* when so contrasted, are seen to differ in a considerable number of ways, chief among them: (a) *P. miradorensis* has less dentate leaves, except for the postical bases; (b) it has more falcate, and considerably more attenuated leaves; (c) the postical base is more broadly and strongly reflexed-convolute, forming a tubular "water-sac"; (d) the postical base is distinctly spinose-dentate; (e) the cells of the postical base are scarcely elongated, and strongly collenchymatous, without marked confluence of the trigones — compare here Fig. 67:10 with 3; (f) the cells of the leaf-apices are nearly isodiametric, without any marked tendency for the cells to be tangentially elongated — and without any tendency for the trigones to be confluent along the longitudinal walls (Fig. 67:8); (g) the underleaves minute, formed of usually 2-4 filiform cilia, uniseriate throughout, or only 2 — rarely 3 — seriate near the base (Fig. 67:14, 15).

Of these differences, *c, d, e* and *g* are the most constant and systematically the most important. These differences were fully as marked in a second "mixed" collection, where the two species grew intimately admixed (*Schuster* 19184a, Black Creek, 8-9 mi. N. of Escatawpa, Miss.), and in a third (*Schuster* 22981, near Van Cleave, Miss.). In extreme shade forms of *P. ludoviciana* (which are, however, very deeply chlorophyllose and opaque) the leaves may be as nearly edentate as in "normal" *P. miradorensis* (compare Fig. 68:6, 10, 17 with Fig. 68:22), and have the cells with small or vestigial trigones. The total lack of any dentition of the cristate postical leaf-bases serves to separate such phases of *P. ludoviciana* from all forms of *P. miradorensis.*

Among the many collections of *P. miradorensis* seen from this area, only one (*Schuster* 19250b) possessed mature perianths. The perianths in this case were not fertilized, and the inner faces, and base, had proliferated "propagula" — a feature also often characteristic of the unfertilized perianths of *P. ludovi-*

ciana. The larger perianths seen were *ca.* 1300 μ wide and up to 2200 μ long. In these the antical keel was sharply, if narrowly, winged for almost their total length, with the wing bearing 3-4 inconspicuous teeth. The mouth, as in *P. ludoviciana,* was obliquely terminated, with the postical keel as a consequence shorter than the antical. The ventral half of the mouth was distinctly undulate-reflexed, again a feature typical of *P. ludoviciana.* The perianth thus closely agreed with that of *P. ludoviciana,* except for one feature: the presence of a more discrete, dentate, antical keel, extending upward for all — or almost all — of the length of the perianth. This feature also characterizes the type of *P. miradorensis.*

By contrast, *P. ludoviciana* (and such presumed synonyms of it as *P. schliemiana, P. plicata, P. schiedeana,* and *P. punctualis*) have an essentially or quite edentate antical keel of the perianth. In *P. patula* and *P. subcristata,* which closely resemble *P. ludoviciana* in other respects, the antical keel of the perianth is widely winged, at least below, and dentate. If the latter prove to be discrete species, *P. ludoviciana* may then be considered to include only populations with the perianth-wing poorly developed and edentate, while *P. miradorensis* has the rather well-developed antical perianth wing armed with several small teeth. Study of much longer series of "fruiting" specimens is needed to substantiate such a suggested difference.

Among the neotropical species restricted to Central and South America, *P. miradorensis* appears to be related most immediately to *P. cucullata* Lindenb. et Gottsche (in G. L. et N., Syn. Hep. 642, 1847). This Mexican species is more fully described and illustrated by Gottsche (1863). As Gottsche has indicated, the later described *P. miradorensis* differs from *P. cucullata* in the much smaller underleaves, which are reduced to 2-several tortuous capillary cilia. Our material, referred to *P. miradorensis,* agrees closely — and apparently uniformly — with *P. miradorensis* in the form of the underleaves. This suggests that the large, laciniate and ciliate underleaves of *P. cucullata* serve to separate it from *P. miradorensis* specifically. Gottsche also cited a further difference: *P. cucullata,* in drying, develops "convoluta corrugataque folia"; in *P. miradorensis* they supposedly do not become convolute in drying. Whether this difference is valid or not is not determinable from the material available.

It is clearly necessary to study a series of specimens from Mexico to determine whether these two differences warrant separation of *P. miradorensis* from *P. cucullata.* For the time being, the former is maintained as a distinct species, largely because no intermediates to *P. cucullata* have been found. It may well prove necessary, however, to treat *P. miradorensis* as a mere variant of *P. cucullata* (as was done in the *Synopsis Hepaticarum,* p. 642, 1847).

The appearance of dry individuals of mature plants of our phases of the *P. miradorensis* complex is most characteristic. The basal, ampliate portions of the leaves are erect and closely sheath the stem — with the consequence that the plant superficially appears to have a very stout stem. By contrast, the narrow, slender, drawn-out portions of the leaves are often convolute and twisted, sometimes forming a slender tube. These twisted distal portions of the leaves, in the aggregate, often give the superficial impression of slender, spreading spur-like appendages arising from a thickened axis.

In weaker plants, this characteristic mode of drying is often not as marked. However, the different aspects of dry plants of *P. ludoviciana* and *P. hypnoides* (which have simply postically secund leaves, in drying) and *P. miradorensis* are always easily evident to the practiced eye. On this sole basis, it was possible to consistently separate individual shoots of *P. ludoviciana* and *P. miradorensis*, when the two grow admixed (as in *Schuster* 19184a).

Variation.—An extraordinarily variable species. The pattern of variation is discussed at length (see discussion under Sectio Crispatae), in conjunction with the differences in variation between this species and *P. ludoviciana.*

The variability in leaf form is so extreme that a diagnosis of the leaf-shape must either be so broad as to be meaningless, or else restricted to more or less "typical" manifestations of the species (as has been done above). In extreme cases (Fig. 68:1-2), the leaf apex and postical margin bear from 12-16 sharp but low teeth, in addition to 4-7 cilia-like teeth of the reflexed basal "flap." Such cases are exceptional and approach *P. ludoviciana* in the dentition. The teeth in *P. miradorensis* are usually more distinctly serrate in nature than in *P. ludoviciana.* Those of the postical margin are all, or almost all, distinctly oblique. To a lesser extent this may be true of *P. ludoviciana.* More frequently the leaves have the dentition much reduced, often to 1-3 teeth near the leaf-apex, with the postical margin edentate or merely sinuate, except for the postical reflexed base, which retains

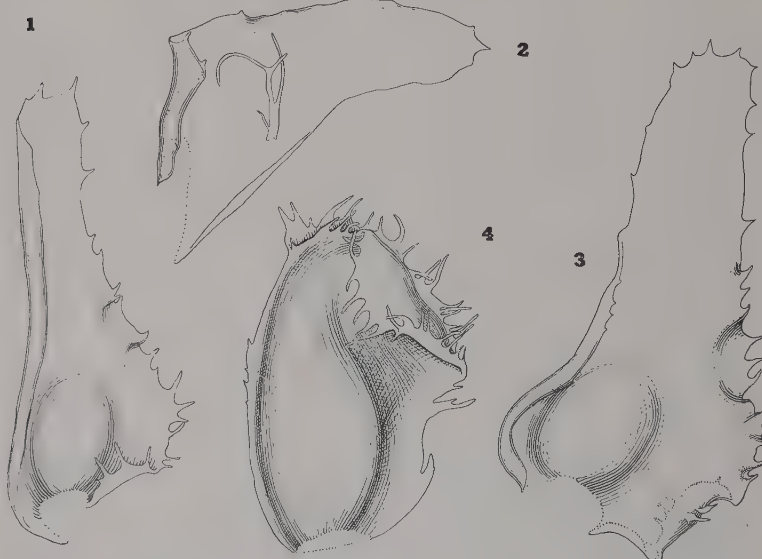

Fig. 70.—*Plagiochila miradorensis* Gottsche. 1, 3. Female bracts (x 21); 2. Stem leaf and underleaf (x 21); 4. Perianth in lateral aspect (x 21). (Figures all drawn from *Schuster* 19250b.)

usually 1-5 sharp teeth (Figs 67: 6-7, 14; 68: 10-11, 15-17). This is to be regarded as the "normal", or at least "common" phase of the species, and is produced under relatively xeric conditions. In both of these forms there is a wide range as to leaf-shape, this ranging from falcate-oblong (Fig. 67:14), with the leaves ca. 1900-2000 μ long x 850-900 μ wide; to ovate-lanceolate (Fig. 68:10-11), with the leaves ca. 1850-2000 μ long x 900-925 μ wide; to relatively broadly ovate-falcate (Fig. 68:6), and up to 2450 μ long x 1475 μ wide. The leaves, in all such forms, are little or not undulate along the postical margin, and are conspicuously, gradually narrowed to the apex. They average consistently from *ca.* (1.65-1.7) 1.85-2.35 as long as wide.

Occasionally, however, totally anomalous phases are produced (Fig. 67: 11-12, 18), in which the leaf is a rounded and abbreviate oblong-lingulate, ranging from 1360-1450 μ long x 1000-1025 μ wide (*i.e.,* only from 1.35-1.45 $\times$ as long as wide!). Shoots with leaves of this type at first glance give the impression of belonging to wholly different species — the leaves being strongly crispate-undulate, with the rounded apices and edentate margins of *P. undata.* However, the transition from this type of leaf to the "normal" type may occur on the same shoot! Fig. 67:6-7 and 11-12 were drawn from leaves of one plant, as were Figs. 16, 18! It is to be noted that the leaf-margins of this anomalous extreme, with broadly oblong-lingulate leaves, are quite entire and broadly rounded at the apex — even the reflexed postical base is usually totally edentate. Why perfectly normal shoots should "go over" suddenly into the oblong-lingulate extreme is not clear. One plant, carefully studied, shows one aerial branch with the leaves consistently of the type in Fig. 67:11-12, 18; on the other aerial branch the basal portion (figured in Fig. 67:16) had similar leaves, with suddenly a cessation of this type of leaf, the distal portions of the shoot showing first short, rudimentary leaves, then "going over" into a sector (illustrated in Fig. 67:18), with leaves strongly reminiscent of those of *P. undata.* A few other shoots, wholly with leaves of this latter type, were also noted.

Only one variant, based on leaf-type, appears sufficiently stable and sharply defined to warrant recognition as a separate variety, var. *convoluta.* This is treated below. Excluding this, the species still remains extremely polymorphous.

Plagiochila miradorensis var. **convoluta** var. n.

Figs. 68:10-15; 69:1-9

Folia tenua, 2.0-2.2 $\times$ longa quam lata, falcata; posticus basis fere brevi-decurrens, in 0.4-0.5 decurrentia antici basis, acute convoluta faciens angustam tubiformam colpam edentatam vel 1-2 parvis dentibus; margines foliorum aliter saepe integrae. Typus: North of Escatawpa, Mississippi (*Schuster* 27759); in herb auct.

Plants in large but loose mats, near the bases of tree trunks, dull green to olive-green, dull-textured when dry, with strong differentiation into creeping rhizomatous shoot system and ascending, arched, leafy stems. Mature aerial shoots subsimple or rarely pseudodichotomous, usually 3.2-3.8 mm wide; stems rigid, brownish, 180-200 μ in diameter. Rhizoids absent, or virtually absent, on aerial shoots. Leaves

strongly imbricate, when dry somewhat postically secund, when moist nearly horizontally spreading, at an angle of 65-85° with stem (the antical margin at an angle of (45) 55-75° with stem; postical margin at an angle of 85-100°); *leaves slender, narrowly, obliquely, ovate to ovate-falcate to lanceolate-falcate,* varying from 1580 μ long x 840 μ wide to 1800-1875 μ long x 900-1000 μ wide, occasionally to 2000 μ long x 900 μ wide (*length averaging* 2.0-2.2 × *the maximal subbasal width*); insertion of leaf unequally U-shaped, the antical insertion ranging from 525-750 μ (0.6-0.8 *the subbasal width*), the leaf thus *antically relatively short-decurrent; postical insertion relatively short-decurrent,* ranging from 225-320 μ (*ca.* 0.4-0.48 the length of decurrence of the antical portion). Ventral margin of leaf moderately ampliate above the short-decurrent base, the margin (from ampliate region) to the apex averaging almost straight and at right angles to stem; margin, from ampliate area to (and including) the decurrent base, *sharply convolute and reflexed to form a well-defined tubular, basal fold;* postical basal folds of the leaves juxtaposed on the stem, *the stem in postical aspect essentially hidden. Leaf-margins subentire,* the narrowly tapering apex usually weakly bidentate (rarely tridentate), but sometimes ending in a single acute tooth; *postical margin, above base, entire to sinuous,* rarely 1-dentate; *convolute basal margin of leaf with often* 1(2) *spinose but small teeth.* Apical and subapical cells *ca.* 18-20 x 23-27 μ, with large, ± bulging trigones; the marginal cells equally collenchymatous, not thick-walled; median cells similar in size, with similar development of collenchyma, occasionally to 18-23 x 27-32 μ; basal median cells 21-23 μ x 28-38 (42) μ, strongly collenchymatous, with bulging trigones (and occasional intermediate thickenings); cells at base of decurrent strip little elongated, similar to cells of median base, similarly collenchymatous, *ca.* (16) 20-21 x 24-33 μ; oil-bodies segmented. Underleaves small, constantly present, formed of 2-several extremely elongate, slender, largely uniseriate cilia, *without any extensive lamellate development. Asexual reproduction freely present,* by means of propagula from the postical leaf surface. Sex organs unknown.

Type.—On bark of *Nyssa sylvatica biflora,* swampy woods 2-3 mi. N. of Escatawpa, Jackson Co., Mississippi (*Schuster* 27759, April 4, 1953). Known only from the type collection.

Ecology.—On bark, on the fluting bases of swamp tupelo, in a semi-evergreen swamp forest (*Taxodium, Cyrilla, Cliftonia, Leucothöe,* etc.). Annual flooding to a height of 2-3 feet, during the spring, with a dry summer and fall period is typical of the site. Associated herbs on the bases of the trees include *Epidendrum conopseum* (at its northern edge in the Gulf Coast) and *Polypodium polypodioides michauxiana.* The reddish-tinged lichen, *Chiodecton sanguineum,* the hepatics *Mastigolejeunea auriculata, Cheilolejeunea rigidula* and *clausa,* and the mosses *Tortella humilis, Leucodon julaceus, Schwetzkeopsis denticulata* were associated.

Differentiation.—*P. miradorensis* var. *convoluta* differs from the typical species in several salient respects: (a) the postical leaf-base is relatively short-decurrent, the decurrent strip extending down for usually less than 0.5 the merophyte length; (b) this postical basal area is sharply, but quite narrowly reflexed, with the reflexed margin usually edentate, more occasionally bearing a single tooth; (c) the antical leaf-margin is unusually short decurrent, compared to the typical plant (and compared to the "normal" members of the Crispatae). These differences initially seemed so impressive that the writer regarded these plants as possibly specifically distinct. Subsequent study of long series of specimens of *P. miradorensis* has demonstrated that the latter frequently produced phases with virtually edentate leaves, whose postical base may bear only 1-2 teeth. Such plants represent a partial transition to the var. *convoluta*.

Study of a series of plants of the var. *convoluta* has shown that occasional leaves may show a decurrence of up to 0.6 the merophyte length. Such instances show that this plant actually belongs in the Sectio Crispatae. However, the unusually short postical decurrence of most leaves at first glance would suggest that the variety does not belong here, but rather in the Hypnoides. However, *P. miradorensis* var. *convoluta* differs from *P. hypnoides* and its immediate allies in the subentire leaves, the development of a water sac at the postical leaf base, and in the underleaves, which are formed of several linear elongate cilia.

In the narrowly convolute, tubular postical leaf-bases, *P. miradorensis* var. *convoluta* approaches the Mexican *P. schliemiana* Gottsche (as figured in Gottsche, 1863, pl. 1). However, *P. schliemiana* has freely dentate leaf-margins, and a long-decurrent postical leaf-base. This "species" may be a mere form of *P. ludoviciana.* The leaf-form, and particularly the tendency for the formation of 2 sharp apical teeth terminating the narrow leaf-apex, suggest a weak form of the tropical *P. connata* Lindenb. and Gottsche (as figured in Gottsche, 1863, pl. 8). However, this plant does not have a convolute postical leaf-base, and both antical and postical leaf-bases are markedly decurrent.

PLAGIOCHILA UNDATA Sull.
Fig. 71

Plagiochila undata Sull., Musci Alleghaniensis No. 222, 1845.
Plagiochila crispata Gottsche Mex. Leverm. Dansk. Vidensk. Skrift. 6:167, pl. 15, 1863 (new synonym).

Since detailed study of type material of *P. undata* and of the putative type of *P. crispata,* as well as of a long series of specimens, indicates that the latter intergrades in some respects with the former, I have here treated the two as representing mere geographic races of a single polymorphic species.

PLAGIOCHILA UNDATA subsp. UNDATA Sull.
Plagiochila undata Sullivant, Musci Allegh. No. 222, 1845.

Plants robust, usually in dense, extensive tufts or masses, the ascending aerial shoots at maturity 2.5-3.5 mm wide x 2-5 cm long.

Plants green, occasionally olive-green to olive-brown with age, never distinctly brown, dull. Stems 225-275 μ thick, occasionally to 300 μ thick, brownish with age in many cases, simple or occasionally 1-several times dichotomously furcate. Leaves closely imbricate, the line of insertion exceedingly strongly arched, insertion U-shaped, the *dorsal leaf-base exceedingly long-decurrent, the postical leaf-base nearly equally long-decurrent, the stem virtually or quite hidden both in antical and postical aspect* (the postical decurrent strip broad, usually strongly reflexed to form a vestigial, tubular, postical pocket, extending down 0.7-0.9 the length of the ventral merophytes); leaves obliquely, asymmetrically ovate to triangular-ovate, spreading horizontally on each side when moist, suberect and strongly postically secund when dry, at an angle of *ca.* 45-65° with the stem-apex, *ca.* 1.7-2.0 (2.1) mm long x 1.2-1.4 mm wide (the length 1.3-1.5 [1.65] × the width); leaf widest just above base, the postical border above decurrent base strongly dilated and arched, the postical leaf-margin distad of the recurved base usually at an angle of (75) 90-110° with stem-apex, nearly straight, but more or less *strongly crispate and undulate, nearly or quite edentate;* the narrowed leaf-apex narrowly truncate or rounded-truncate, *bearing* 0-3 (4-5) *obscure to small teeth;* antical margin above decurrent strip nearly straight, but evenly convergent to postical margin, the leaf thus more or less evenly narrowed distally, strongly reflexed for from 0.6-0.9 its length, edentate throughout; median base of leaf strongly depressed, the depression extending out as a broad and shallow sulcus for 0.4-0.6 the leaf-length, resulting (with the reflexed antical margin) in a pronounced convex, inflated appearing dorsal fold or cnemis. Cells of leaf-apex *ca.* 18 μ, of leaf-middle 21-23 μ wide x 28-33 μ, thin-walled to slightly thick-walled with large to distinctly bulging trigones; intermediate thickenings absent; basal cells little wider along midline, *ca.* 18-23 x 27-36 μ, somewhat more elongate but not forming a basal vitta, less than twice as long as wide (on an average); oil-bodies of leaf-middle mostly 4-9 per cell, when few per cell ellipsoidal to ovoid and 5 x 7.5-9 μ, when more numerous often nearly spherical and 4-4.5 μ to 4.5 x 6 μ, formed of rather numerous strongly protruding spherules *ca.* 1-1.2 μ in diameter (22-40 in large oil-bodies in face-view), colorless and rather translucent; chloroplasts averaging smaller than oil-bodies, *ca.* 4.5-5 μ long. Underleaves rather small, lanceolate and with 1-2 marginal (usually subbasal) uniseriate cilia, or bifid and ending in ciliary segments, or divided into 2-5 largely uniseriate cilia, polymorphic. *Asexual reproduction usually absent,* exceptionally with propagula.

Male plants with androecia either intercalary on long, leading branches, or basal on each fork of a furcately (terminally) branched leading axis, then geminate; in either case the androecia becoming intercalary, the axes potentially again fertile and often soon producing secondary androecia. Androecia very compact, spicate, the bracts densely imbricate, commonly in 8-12 pairs; bracts smaller and less typically developed near base and apex of androecium, the androecia

thus somewhat narrowed basally and usually markedly narrowed at apex, below the vegetative proliferation; bracts with basal half strongly ventricose, the median portions erect and imbricate, only the distal parts of antical margin and the apex spreading and often reflexed; postical bases of bracts decurrent like leaves, and the postical margins strongly crispate like those of leaves (diagnosis based on a plant from Orizaba, Mexico, *Farlow, 1885,* which agrees perfectly with subsp. *undata*). Female inflorescences terminal on main shoot, *normally with 1-2 innovations.* Bracts *ca.* 2.6 mm long x 1.7 mm wide broadly ovate-triangular, the base closely sheathing perianth, the dorsal reflexed margin sometimes slightly denticulate; *ventral margin and apex with scattered, small teeth;* postical margin and base usually very strongly crispate. Perianth in lateral view wide-mouthed, almost obcampanulate in outline, laterally compressed above and dorsally keeled (but apparently not with keel winged); mouth bilabiate, ciliate to ciliate-dentate.

Type.—Along Savannah R., Ga. (*W. S. Sullivant,* Musci Alleghaniensis, No. 222, 1845).

Distribution.—ILLINOIS: Southern part of state (Drexler, 1936; according to Frye and Clark, 1944). NORTH CAROLINA: Falls of the Yadkin R., Stanley Co. (*Small* 9683!; as *P. ludoviciana* in herb. Yale); Swamp forest, 1.5 mi. E. of Whiteville, Rte. 74-76, Columbus Co. (*Schuster, Blomquist and Bryan* 29981, 30001; 30001b with *P. dubia*); along Eno R., *ca.* 5 mi. NW. of Durham, Durham Co. (*Schuster* 37480, 37482, 37455, 37482, 37480a; *Schuster and Blomquist* 28216a); along New Hope Creek, Orange Co. (*Schuster* 38197; *Blomquist* 7314!); Linville Caverns, S. of Linville, McDowell Co. (*Anderson* 11029!); Silver Mine Creek, near Hot Springs (*M. S. Taylor* 2361!). (Early reports of the species from North Carolina, based on plants from "Salem" [Winston-Salem], leg. *Schweinitz!,* in the "Herbarium of Columbia College" [NYBG] are based on plants of *Plagiochila yokogurensis fragilifolia.*) SOUTH CAROLINA: Ravine of Estatoe Creek, N. Pickens Co. (*Schuster* 37669, 37669a, with *P. ludoviciana;* 37656a, 37677, 37676, with *P. ludoviciana*); gorge of Whitewater R., S. of Lower Falls, *ca.* 3 mi. N. of Jocassee, Oconee Co. (*Schuster* 27830). TENNESSEE: Lake Calderwood, Blount Co., 975 ft. (*Sharp* 397!); Lake Calderwood, Monroe Co., 975 ft. (*Sharp* 3910!; *c. perianth*!); Walker's Valley, Blount Co., 1400 ft. (*Sharp* 34198!; also issued *in* Verdoorn, Hep. Select. et Crit. *Nos.* 389, 479!); Hiwassee Gorge, Polk Co., 1000 ft. (*Sharp* 160!). GEORGIA: Gorge below Tallulah Falls, Rabun Co. (*Schuster* 34366); Toccoa Falls, N. of Toccoa, Stephens Co. (*Schuster* 25089); Toccoa Falls (*Lesquereux, 1850; L. M. Underwood, Apr. 20, 1891* — Underwood and Cook, Hep. Amer. No. 108!); N. face of granite cliff, Clarke Co. (*R. M. Harper, June 27, 1900*); shaded banks of rivers and wet rocks (*Sullivant, Lesquereux,* Hep. Borealis-Americanae, Austin 1873, No. 10!); Magnolia Park, Thomasville (*C. C. Haynes* 2988! p. p., mixed with *P. ludoviciana*); Seventeen Mile Creek, Coffee Co. (*R. M. Harper* 2047, 1448c, 2047a!); Chattahoochee Co. (*Roland M. Harper* 1795a!); Brooks Co., near Okapilco Creek (*Roland M. Harper* 1625a!); Dade Co. (*Carroll,* 1945). FLORIDA: Gainesville (*N. L. T. Nelson* 115!); Rock Park, Apalachicola R., Torreya State Park, Calhoun Co. (*Anderson* 5186!); Citrus, Highlands, Polk and Seminole Cos. (Redfearn, 1952); Alum Bluff, Liberty Co. (*McFarlin,* 1935); material from Sanford, Orange Co. (*Rapp*), Sanford (*S. Rapp* No. 14) det. Evans = *P. miradorensis.*

The McFarlin and Redfearn reports need verification. ALABAMA: (*F. E. Lloyd, F. S. Earle, Sept. 1900!*); Tuscaloosa, Tuscaloosa Co. (*Pollard and Maxon* 316!; as *P. ludoviciana* in herb. Yale; a green, slightly shiny mod. *viridis-leptoderma,* with the leaves virtually edentate and the postical leaf-margins with weaker than usual undulations). MISSISSIPPI: Among *P. ludoviciana* (*Schuster* 26796a) on bark of Beech, Wyatt Hills, NE. of Ramsey Springs, W. George Co. (*Schuster* 26796). LOUISIANA: Chinchuba (*A. B. Langlois, April 20, 1891!*); Fricke's Cave, Folsom, bases of trees (*Mackaness, Mar. 9, 1941!*). ARKANSAS: Sandstone, 8 mi. NW of Boxley, Newton Co. (*Anderson* 12123!); "Lost Valley," 2 mi. NE. of Boxley, alt. 1000 ft. (*Iltis and Moore* 4197); Camp Albert Pike, Little Missouri R., N. of Langley, Ouachita Mts., Montgomery Co. (*Anderson* 11381a!, 11378!).

The report of *P. undata* from Illinois (Frye and Clark, *loc. cit.*) should be verified. On phytogeographic grounds it appears improbable that the species should occur in Illinois.

Variation.—The subspecies is relatively stenotypic, compared to *P. ludoviciana,* but appears to show a considerable amount of variation in two chief directions: (1) Development of marginal teeth. Typically, the rounded to subtruncate leaf-apex bears no teeth, or occasionally 1-3, rarely 4 minute, obscure denticulations (Fig. 71:1, 3). Occasionally the apical teeth are 4-5 in number (Fig. 71:4), as in the material from St. Martinsville, La., at Chinchuba (*Langlois,* 1891, NYBG), and then the postical margin may show traces of a few. Similarly, material from Florida (figured by Kurz and Little, 1933) shows 3-5 apical, rather discrete teeth. Such plants, with evident denticulation, represent intergradations to *P. u. crispata.* (2) Degree of development of the undulation of the leaf. Typically, the subspecies *undata* shows a few, broad, relatively salient undulations of the postical leaf-margin, while the base may be undulate-reflexed. Occasionally the undulations are less marked individually, but more numerous (again showing intergradation to *P. u. crispata*).

The dentition of the leaves appears to be most marked in small, xeromorphic phases. For example, a collection from Orange County, North Carolina (*Blomquist* 7314, p.p., among *Radula andicola*), of small, brownish-olive plants only 2.2-2.6 mm wide, has the leaves with strongly developed teeth. Most leaves bear 3-5 sharp teeth apically, some of which are 2-3 cells wide x 3-5 cells long, rarely attaining a length of 5-7 cells. Such leaves are more or less repand-crenate to repand-undulate along the strongly crispate-undulate postical margin and base, and occasionally bear well-marked teeth along the postical margin. Even more critical are the plants from the Falls of the Yadkin River, North Carolina (*Small* 9683; Yale; determined by Evans as *P. ludoviciana* evidently on the basis of the strong dentition), in which the leaves are rather atypically drawn out and longer than normal, and in which the dentition is even more strongly marked. In these plants the leaf-apices together with the subapical regions may bear 6-7 sharp teeth 2-4 cells long and 2-4 cells wide at base; the strongly crispate postical margins are also provided with conspicuous, if not very large teeth. The dentition of the leaves is much more marked than in the

Mexican plants of *P. crispata* illustrated in Gottsche (*loc. cit.*, pl. 15), although the female bracts are no more strongly toothed than the leaves. This suggests that the dentition of the leaves does not warrant separation of *P. crispata,* and that any separation, if attempted, must be on the basis of the much more conspicuous dentition of the female bracts. The Small collection is also deviant in that the decurrent postical leaf-bases are conspicuously tubularly reflexed, with the apices of the tubular portion normally marked by a sharp tooth on mature leaves. In both the dentition and sharply reflexed postical bases these plants closely approach *P. miradorensis* from which they are immediately separable on the basis of the strongly crispate leaves.

Perianths are rather frequently developed in this species, although rarely well developed. They often are situated in the fork of a dichotomy, *i.e.,* surpassed by two strong, equal subfloral innovations. Juvenile perianths often are strongly bilabiate, with both antical and postical keels obscurely developed. Each "lip" typically bears 25-30 unequal sharp teeth. By contrast, propagula are rarely developed. I have seen only one collection with them present in any numbers (Orange County, North Carolina, *Schuster and Blomquist* 28197), in which they were strictly limited to the postical leaf faces; a few occur in *Small* 9683. Evidently a much stronger stimulus is needed for propagulum-development in this species than in the allied *P. ludoviciana* and *P. miradorensis,* since when *P. undata* occcurs with the former it is normally propagulum-free while the *P. ludoviciana* is abundantly propaguliferous.

Ecology.—This robust species occurs chiefly in the Piedmont and in the escarpment region, between the Piedmont and Appalachian Highlands, where it may be abundant (particularly in shaded, damp gorges); it is less frequent on the Coastal Plain (where it is largely replaced by the related *P. ludoviciana*). Unlike *P. ludoviciana,* the species occurs most commonly, and most luxuriantly, on shaded, dry to barely damp rocks (where it is found, as at Toccoa Falls, most often with *Porella pinnata, Radula obconica, Leucolejeunea clypeata*). Under the latter conditions, the *Radula* and *Leucolejeunea* are often pioneer, under drier conditions, while *Metzgeria conjugata* is pioneer under moister conditions, and the *Plagiochila* comes in secondarily, after a thin layer of humus has accumulated; at other times, the *Plagiochila* and *Porella* appear to be pioneer. With the development of thick, pure tufts of *P. undata,* soil accumulates, and the *P. undata* mats often serve as a matrix in which ferns (particularly *Asplenium trichomanis;* under very dry conditions sometimes *Polypodium polypodioides*) undergo ecesis.

On dry rocks the species often occurs on both the vertical and weakly sloping faces, sometimes in partial sun. It is then often associated with such xerophilous mosses as *Hedwigia ciliata* and *Grimmia* spp., and with various pioneer lichens.

In the writer's experience, the rock populations of the *Plagiochila* usually serve as a reservoir population for invasion of nearby tree-bases, on which we occasionally find the species (much as is usually the case with *P. ludoviciana*). At Toccoa Falls, for instance, the bark

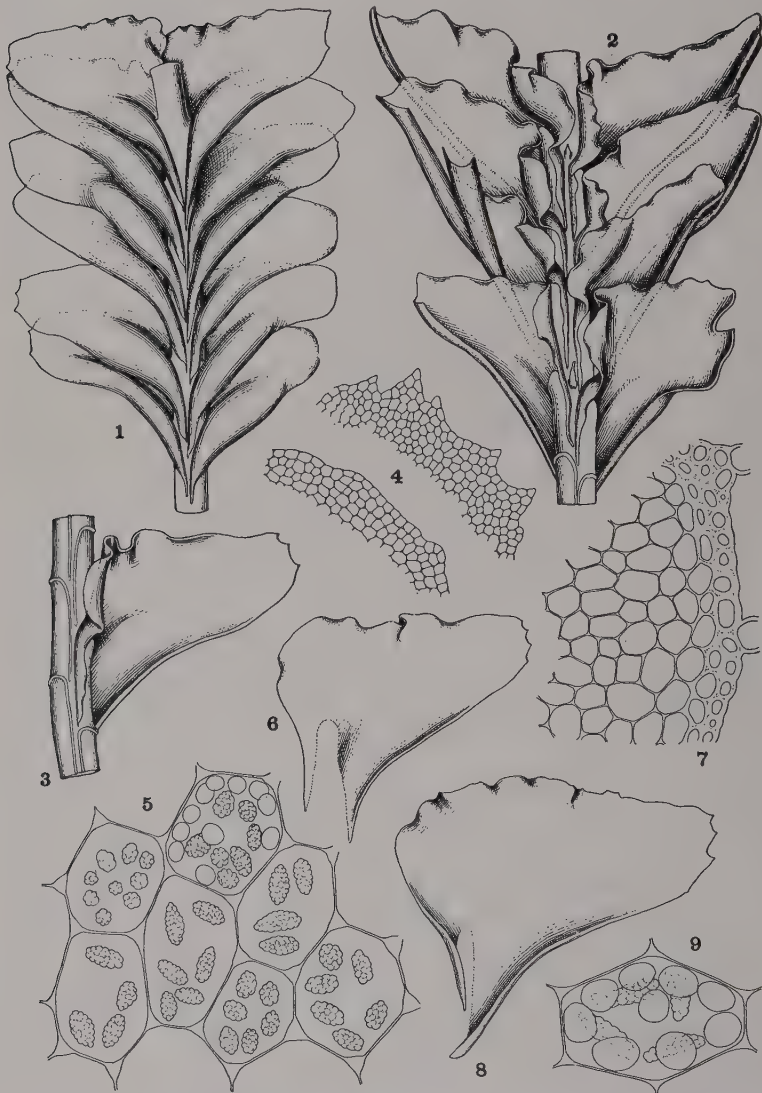

Fig. 71.—*Plagiochila undata* Sulliv. 1. Shoot-sector, antical aspect (x *ca.* 16); 2. Same, postical aspect (x *ca.* 16); 3. Leaf, *in situ,* showing lines of insertion of leaves (x *ca.* 20); 4. Apices of two leaves, showing variation in dentition (x 64); 5. Median cells with oil-bodies (x 500); 6. Leaf (x *ca.* 20); 7. Part of stem cross-section (x 150); 8. Leaf (x 27); 9. Median cells with oil-bodies (x 935). (Figs. 1-3 drawn from type specimen; fig. 5, Toccoa Falls, Ga., *Schuster;* 6, Chunchulla, St. Martinsville, La., *Langlois;* 4. North Carolina, *Schuster* 28197; 7-9, Wyatt Hills, Mississippi, *Schuster* 26796.)

of beeches is often invaded, near the base of the trunk by mosses, *Frullania squarrosa, Polypodium polypodioides, Leucolejeunea clypeata,* and by the *Plagiochila*. When growing on bark, the *Plagiochila* is almost invariably less well-developed than when growing on rocks.

The widespread occurrence of the species (and its occurrence as Massenvegetation, as at Toccoa Falls), is somewhat inexplicable in view of the fact that prolonged search has not revealed the presence of any common mode of either asexual or sexual reproduction. In the apparently nearly total lack of propagula of the leaf-surface we find an excellent means of separating the species from the related *P. ludoviciana*.

Differentiation.—This large and handsome species can scarcely be confused with any other regional *Plagiochila*. The leaves are very usually subentire, or merely obscurely 2-3 (4-5) toothed apically. On this account, and because of the large size, the species may be confused by the beginner with *P. asplenioides* and its relatives. However, *P. undata* at once differs from these in the undulate to undulate-crispate postical margin of the leaf, with the base strongly reflexed, and often crispate and exceedingly long-decurrent. The leaves are characteristically closely imbricate, and consequently the long-decurrent antical, strongly convex basal "folds" of the leaf are usually so strongly approximated that neither postical nor dorsal stem surface is evident (Fig. 71:1-2).

The species is evidently allied most closely to *P. ludoviciana,* with which it shares an exceptionally long-decurrent postical leaf-base (on normal, well-developed plants the arched, decurrent line of insertion running down the stem nearly to the arched portion of the line of insertion of the leaf below it); reflexed postical leaf-bases; ovate-triangular leaves that are widest near base and long-decurrent dorsally; noncaducous leaves, etc. But *P. ludoviciana* differs at once from *P. undata* in: (1) the more or less spinous-dentate postical leaf-margin distad of the reflexed base; (2) the more or less strongly spinous-dentate distal portion of the leaf; (3) the noncrispate and nonundulate postical leaf-margin; (4) the general abundance of "brood-branchlets" on the lower leaf surface.

The absence of strong and obvious dentition of the leaves, as well as the long-decurrent postical leaf-base, serves at once to separate the species from the rest of our *Plagiochila* species.

The closest relative of *P. undata* is undoubtedly *P. crispata* Gottsche (Mex. Levermosser 71, pl. 15, 1863), and Evans (1896, p. 193) refers the latter, with some doubt, to *P. undata* as a synonym. Evans correctly points out that the differences between *P. undata* and *ludoviciana* are differences of degree, rather than kind. Typically, *P. crispata* has the postical leaf-margin more strongly and regularly crispate-undulate, than in *P. undata,* the plants showing in postical view a leaf-form and orientation that is even more involved and complex than in the regional forms of *P. undata*. However, in addition to the greater degree of wavyness of the anterior leaf-margin, *P. crispata* typically also shows a stronger development of the teeth of the leaf-margins. In our local *P. undata,* the leaf-margins are usually suben-

tire, the subtruncate apex occasionally showing poorly developed traces of teeth. By contrast, a "typical" specimen of *P. crispata* from "Mexico, 3000-8000, Fr. V. Müller" (NYBG, ex herb. Wm. Mitten) shows leaf-margins where the apex bears 3-4 small teeth; the distal part of the antical margin often bears 1-2 teeth, and the postical, crispate margin may bear 2-3 or more teeth (often difficult to demonstrate unless the leaf is flattened out). Stephani (Spec. Hep. II:323, 1903) also emphasizes this difference for the floral leaves stating: *"Plagiochila crispata* G. differt foliis floralibus grosse remoteque spinosis et perianthi ore valide et longe spinosa mecon foliis caulinis apice distincte denticulatis." In *P. undata* the perianth is *ca.* 2 mm long x 2 mm wide, flattened, but campanulate in outline, somewhat bilabiate, with the lips merely ciliate, not spinose-ciliate. The bracts are similar to the leaves, but have the deflexed antical margin "denticulate, postical margin and apex irregularly dentate" (Evans, 1896).

It is therefore evident that *P. crispata* has a strong tendency to develop marginal teeth of the leaves, with the bracts and perianth-mouth becoming spinose; by contrast, the leaves of *P. undata* are typically subentire, while the bracts become denticulate to dentate, and the perianth-mouth merely ciliate. As is evident, these differences, too, are merely of "degree, and not of kind." In addition, I have studied specimens with strongly crispate leaves, which bear more obscure teeth (3-6 per leaf with 1-2 on many of the crispate postical margins), such as a specimen of *"P. crispata"* from Orizaba, Mexico, 1885 (W. G. Farlow), in herb. Yale and NYBG, which evidently bridges the gap between the *crispata* extreme and *undata* extreme. For that reason, it seems that *crispata* represents merely a southern, regional manifestation of what the writer would regard as a more broadly conceived *P. undata*. Under these conditions, it seems reasonable to propose a new combination:

Plagiochila undata subsp. **crispata** (Gottsche) new comb.
Plagiochila crispata Gottsche, Mex. Levermosser 71, pl. 15, 1863.

Specimens examined.—Mexico, 3000-8000 ft., Fr. V. Müller.

In addition to the above specimen of the subspecies *crispata* that I have studied, I have also seen a specimen from Panama (labelled *"crispula"* on the packet), in the Mitten Collection (NYBG). This specimen, very fragmentary, clearly belongs to *P. undata,* but differs somewhat from both *P. undata* subsp. *undata* and the subsp. *crispata* in having the postical leaf-base, just above the decurrent portion, exceedingly strongly dilated. The dilated base is also usually not reflexed, but more generally lies flat or stands slightly away from the postical stem-surface. As a consequence, the postical stem-surface is completely hidden, and the dilated postical leaf-bases may be quite strongly imbricate. This form, in the writer's opinion, should possibly also be recognized as a discrete race. I have also seen another specimen from Panama (Wm. Seeman), in the NYBG, labelled *"Plagiochila crispula* Lindb."; this is filed with *P. crispata* Gottsche. The specimen appears quite inseparable from *P. ludoviciana* Sulliv.

P. undata (in the broad sense) is related clearly to several tropical species, among them *P. crispata-decurrens* (Herzog, 1932, p. 214). The latter shows an even greater development of the decurrent postical leaf-base, which is crisped rather than reflexed to form a water-sac, and has an excessively long-decurrent antical leaf-base. This species also shows large underleaves that are profoundly bilobed and more or less dentate at the bases of the lobes. Some relationship of *P. undata* also exists with the South African *P. crispato-caudata* G., although this relationship is more diffuse.

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A Preliminary Analysis of Habitat Orientation in Microtus and Peromyscus[1]

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Introduction

Each species of organism is restricted in distribution by the limits of its tolerances to the physical and biological factors of its geographical range. In addition, each species is seldom found everywhere within the limits fixed by these tolerances, but appears to be further restricted to certain microhabitats within its environment. This paper is concerned with the orientation of the white-footed mouse, *Peromyscus leucopus noveboracensis* (Fisher), and the meadow mouse, *Microtus p. pennsylvanicus* (Ord), to microhabitats in stages of old field succession on the Piedmont of New Jersey.

This secondary succession proceeds from previously cultivated land through several seral stages. The earliest stages are dominated by annual herbs, chiefly *Ambrosia* and *Oenothera,* but they also contain the subsequent herbaceous dominants in small numbers. By the fifth year several species of *Solidago* and *Aster* have become dominant and generally remain prominent for another 15 years. Broomsedge, *Andropogon scoparius,* reaches dominance by the fifteenth year and remains so for about 45 years. The red cedar, *Juniperus virginiana,* seeds early in the succession and remains the dominant arborescent species for over 60 years. The cedars are joined by the dominant species of a mature oak-hickory forest by the fifteenth year. These oaks are well established in the understory by the sixtieth year, and later constitute the climax forest in this region. *Myrica pensylvanica* and *Rubus flagellaris* are the dominant shrubs in the fields until the twentieth or thirtieth year, when *Rhus radicans* becomes prevalent and remains so to the oldest fields observed.

A series of fields in Franklin Township, Somerset County, New Jersey, represents all the seral stages in this succession. These fields are found on soils of the Norton series formed over the Brunswick formation of the Triassic shales comprising a part of the Piedmont Plateau. A study by Bard (1952) determined the major changes in vegetation occurring throughout the succession discussed above. The results of this study provide an accurate description of the plant variation and the habitat changes.

In 1957 a study of the small mammal populations associated with the secondary succession in these fields provided a foundation for the present project (Pearson, 1959). In addition to indicating the species

[1] This paper is part of a Rutgers Scholar thesis on undergraduate research by the senior author, and directed by the junior author.

present and the relative population levels in the several seral stages, this study established certain patterns of mammal distribution relative to vegetational cover. The results of Pearson's study point out that captures of the white-footed mouse were associated with perennial forbs in the early stages and with shrubs and trees in the late seral stages, and that captures of the meadow mouse and masked shrew, *Sorex c. cinereus* Kerr, were associated with the dense broomsedge cover found in the 7, 11, and 16 year stages.

The present study was conducted in the series of fields studied by Bard (1952) and later by Pearson (1959). The "age" of these fields, as indicated in Bard's study, was the number of years since the land was last cultivated, and the only difference in the habitats used by these three studies was the difference in "age". The "ages" of the fields in this study were 10, 14, 19, and 24 years and each of these was 9 years younger at the time of Bard's study. However, her study included fields approximating the seral stages used in the present study so that reference is still valuable.

This study consisted of four integral parts. The first, running from September 21 to November 7, 1958, was a census to determine the present population levels, to verify the previously determined associations, and to obtain animals for controlled laboratory experiments to be conducted during the winter. The second phase, in the laboratory, was the construction of an artificial habitat in which association could be further tested. The next part was a series of tests to determine the aggressive tendencies of the two species, and the final phase was a release and retrap study carried on from March 8 to March 19, 1959.

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METHODS

Field Study.—Seventy-five traps were set three nights a week during the fall trapping period. Sherman live traps baited with peanut butter were used. Three parallel lines of 8 or 9 traps, approximately 100 feet apart, were placed in each field. Within each line the traps were spaced at approximate intervals of 50 feet. A series of 25 traps remained in a field for the three nights. Traps were run each morning and replenished with bait or dry cotton if disturbed by the weather or a captured animal. During the fall trapping period all of the animals were removed for use in the laboratory. A careful record of the microhabitat immediately surrounding each trap was kept so that the cover most frequently inhabited in these fields by each species could be determined. A record was kept of the date of capture, the sex and species, and the location of capture for each individual. *Peromyscus* and *Microtus* were marked for future identification by the toe-clipping method described by Pearson (1959). All males captured were immediately isolated from each other by an arrangement described later.

During the spring trapping period, in which all animals were released at the point of capture after marking, the traps were set for 10 consecutive nights. They were placed at 50-foot intervals in a grid coverage of the entire field. The traps were again checked early each morning. All the animals held over the winter were released in these fields, and no animals were again removed. Any new individuals captured were marked and immediately released at the point of capture, as were all the recaptures of previously marked individuals.

Habitat Association.—To determine if there was any habitat association exhibited by the two species an artificial habitat measuring four feet on each side was constructed. Its walls were one foot in height and the top was covered with weathered one-half inch hardware mesh. The floor of the whole enclosure was covered with finely sifted sand. This box was divided into two equal compartments with a joining passage. One side simulated the goldenrod-aster habitat and the other the broomsedge. A wooden cubicle approximately one-foot square fit smoothly into the passage, and the animal to be tested was placed within the cubicle. After a one-minute orientation period the cubicle was silently raised, and subsequently removed, allowing the animal unimpeded choice of either simulated habitat, and also free passage between them.

Ordinary drinking straws were used to simulate the upright stems of the goldenrod-aster habitat. They were placed at four-inch intervals in parallel rows four inches apart; the axes of the individual straws being on a diagonal with, rather than perpendicular to, the sides of the enclosure. Additional straws and a small amount of excelsior were scattered on the sand to simulate the litter. Six bunches of excelsior simulated the clumps of *Andropogon*, and a mat of mixed excelsior and straws was spread over the broomsedge habitat to represent the type of cover found in the field.

An opening with a flush door was placed in a corner of each compartment so that the animal, in its natural wanderings along the wall, could wander out of the artificial habitat of its own volition after the timed trial was ended.

The observer sat motionless at one side of the habitat for half of the trials, and moved to the other side for the second half. The lighting was either natural or from a small ceiling bulb in the center of the room. Neither means lighted the habitat directly. The initial choice of habitat, and the time spent in each simulated habitat were recorded for five-minute trials. Notes were kept on the actions of each animal in the habitat during the trial. No animal was tested more than twice in one day.

Aggressive Behavior.—In order to accurately determine the aggressive tendencies of these two species, the males were, as previously mentioned, kept in isolation from the time of capture. No experiments were run for more than a month after capture. Sixteen cages were built into one unit in two rows of eight. The eight pairs were sepa-

rated by sliding aluminum partitions. Two sides of each compartment (each 6″ x 12″ x 8″) were of wood, the third was the metal partition, and the fourth contained a hardware mesh access door, while the top and bottom were of the same wire mesh. Each compartment was provided with cotton nesting material, a water bottle, and a diet of Purina Laboratory Chow, supplemented by fresh fruit and vegetables. Meadow mice were placed in one side and white-footed mice in the other. All females and extra males were retained in large holding cages on the same diet. Only males kept in isolation were used in the aggression studies.

Five-minute trials were run in these experimental cages with no change other than removal of the nesting material. The cage was illuminated by a single shaded bulb suspended six feet above the cages, and the observer again sat silently at one side for half of the experiments and moved to the other side for the second half. The partition was removed and all actions of the two individuals were recorded for the timed period.

Behavior was divided into the following main classifications: 1) actual fighting, 2) aggressive, 3) recessive, 4) fraternal, 5) sniffing, and 6) no conclusive reaction. It was felt that all actions of the animals would fall into one of these six categories. In actual fighting records were kept on which animal initiated the fighting. Squeaking, chasing, scratching and nipping were classified as aggressive behavior. Recessive behavior included wild leaping, clinging to the roof wire, crouching in the corner with eyes closed, or assuming a defensive position similar to that of a human boxer. Also included as recessive was flight from any act of aggression. Mutual grooming or huddling together were considered fraternal behavior. Those actions grouped as no conclusive reaction generally occurred when the animals passed each other, usually going in opposite directions, and there was opportunity for reaction but none appeared. Each of the males was tested with every other male in a round robin fashion, both within the same

TABLE I.—A summary of total trap-nights and captures with regard to habitats in the fall and spring trapping periods

		Trap-nights	*Peromyscus*	*Microtus*	*Blarina*	*Sorex*	*Mus*
FALL	Andropogon	609	14	12	18	4	..
	Solidago-Aster	198	6	1	..	1	..
	Shrubs	155	5	3	..	..	..
	Misc.	88	4	..	3	1	1
	Total	1050	29	16	21	6	1
SPRING	Andropogon	530	19	..	2	..	1
	Solidago-Aster	140	9	..	..	..	..
	Shrubs	30	3	..	..	..	..
	Misc.	50	..	..	..	..	..
	Total	750	31	..	2	..	1

species and with the other species. No individual had more than two encounters in any four-hour period.

RESULTS

Field Study.—The results of 1050 trap-nights covering the fall trapping period are summarized in Table I. All species recorded by Pearson (1959) except *Pitymys* were captured. Computation of the number of trap-nights necessary for the capture of one individual, as taken from Table I, indicates that although the white-footed mouse was captured in all habitats it was most prevalent in the goldenrod. The meadow mouse and the short-tailed shrew, *Blarina b. brevicauda* (Say), were limited in their range, occurring most frequently in the broomsedge habitat. The catches of the house mouse, *Mus musculus* Linnaeus, and the masked shrew were not large enough to be included in the habitat association analyses. The table also reveals that the white-footed mouse was taken more frequently in all habitats than any other species. Moreover, there was a greater number of captures for all species in the broomsedge.

Statistical examination of the above-mentioned associations may be obtained by submitting the trapping data of Table I to a four-fold chi square test of the association between trap-nights of capture and no-capture versus broomsedge and goldenrod habitat. When this was done for *Peromyscus* no significant association was found ($\chi 2=0.1$, $P=0.7$). Similarly no significant habitat association was found in this test for *Microtus* ($1\chi 2=1.2$, $P=0.3$).

The low trapping success of this study made it readily apparent that there had been a significant decrease in small mammal populations as compared to the earlier work of Pearson (1959). This was

TABLE II.—A measure of relative population levels is given where the figures represent average number of individuals caught per census period per 100 trap-nights. The figures in parentheses are for the same fields as reported by Pearson (1959).

	"Age" of field in years			
	10	14	19	24
Total Trap-Nights	225(622)	225(625)	225(597)	375
Peromyscus	0.15(3.2)	0.29(0.2)	1.78(3.3)	1.47
Microtus	0.15(2.8)	0.45(3.7)	...... (5.5)	0.40
Blarina	1.18(0.6)	1.03(1.3)	0.45(1.0)	0.67
Sorex	0.15(0.6)	0.45(1.3)	...... (0.5)	......
Mus	...... (0.2)	...... (1.6)	0.15(0.1)	......
All species	1.63(8.2)	2.22(8.0)	2.37(10.5)	2.54

specially true for *Microtus* for they had been quite abundant in the earlier study and considerable effort was expended to get the few males needed for the experimental phase of the present project. However, a comparison of trapping success in the two studies is difficult since a mark-and-release procedure was used earlier for all except *Blarina* while all the animals were removed from the field during the fall in this study. It is seen in Table II that there was little change in the *Blarina* population level from the earlier level.

Even though the indices of population size are not directly comparable for the two studies the data in Table II do show what was also concluded while the field work was underway. That is, there was a significant drop in small mammal population levels. For example, no *Microtus* were taken in the 19-year field where they were most abundant two years before, and their populations were only 60 to 70 percent that of the previous study in the other fields.

It should be noted that the population level, or standing crop of small mammals, increases through the early stages of succession as is apparent from the data in this study, as well as that in Pearson's earlier census.

The results of the spring retrap period, after all laboratory animals had been released, are given in Table I. Three meadow mice were released; they were not retaken and there were no new captures. The white-footed mouse was still the most abundant small mammal and, on the basis of trap effort necessary to catch one individual, it appeared to have a higher population level than in the fall. It was captured with less effort in the goldenrod habitat than in broomsedge. The population level of short-tailed shrews was apparently very low as only two individuals were taken.

Table III.—An analysis of the number of changes made from one simulated habitat to the other; an even number of changes indicates that the animal ended in the habitat of original selection.

Number of changes from original habitat selected	*Peromyscus* Initially Selected: Broomsedge	Goldenrod	*Microtus* Initially Selected: Broomsedge	Goldenrod
0	9	10	30	3
1	5	5	..	2
2	1	5	5	..
3	2	..	1	1
4	2	1	3	1
5	..	3	..	3
6+	3	2	1	..
Total	22	26	40	10

Habitat Orientation.—Of the 50 artificial habitat trials run, the meadow mice moved initially into the simulated broomsedge habitat in 80 percent of the trials (Table III). They spent 206 minutes in this habitat (82% of the total trial time), and 44 minutes in the simulated goldenrod habitat. In initial habitat selection the white-footed mice showed a random orientation (Table III). They also spent nearly equal time in the two habitats, with 106 minutes in the simulated broomsedge and 133 minutes in the simulated goldenrod.

The data given above and in Table III were tested by chi square to determine whether the observed frequencies of habitat selection and time spent in habitats differed significantly from an hypothesis of random orientation. Analysis of the *Microtus* data indicated significant deviation from random selection on the initial direction of habitat choice ($\chi^2=18$, $P<0.001$) as well as for the total time spent in the two simulated habitats ($\chi^2=105$, $P<0.0001$). Both of these tests verify a positive orientation of *Microtus* to the simulated broomsedge habitat. Analysis of the original choice of habitat and time spent in each for *Peromyscus* gives no evidence of other than random orientation ($\chi^2=0.33$ and 0.23). Thus it appears that there was no positive association between *Peromyscus* and a simulated habitat.

An analysis of subsequent changes in habitat occupancy after the initial movement for the two species is instructive. In 30 of the 40 trials where *Microtus* moved initially into simulated broomsedge the animal remained there for the duration of the five-minute trial (Table III). Also, of the 40 that moved initially into broomsedge only one ended the experiment in the simulated goldenrod habitat. Of the 7 *Microtus* trials where the animal initially chose the goldenrod habitat but later went to the simulated broomsedge, only one returned to goldenrod. There was an average of 1.18 changes of habitat per five minutes for *Microtus*. In contrast there was an average of 2.08 habitat changes per trial for *Peromyscus*. The number of *Peromyscus* remaining in the habitat of initial choice was about equal for both simulated habitats. The number that moved and ended in the habitat opposite to the initial choice was equal also.

During these trials individuals of both species moved chiefly along the walls of the enclosure, particularly on the side simulating the goldenrod-aster habitat. There was movement beneath the excelsior mat in the simulated broomsedge habitat, particularly by the meadow mouse. Animals frequently remained motionless in the corner for long periods in the goldenrod-aster habitat, and there was a tendency for the meadow mouse to remain motionless under the excelsior mat in the broomsedge habitat.

The subjects seldom bolted upon removal of the cubicle, and on occasion remained motionless for as long as two minutes, indicating that the initial response was not motivated by fear. No attempts were made to climb the drinking straws, but the white-footed mice did occasionally climb the enclosure walls and also climbed on top of the excelsior mat in the simulated broomsedge habitat. The animals fre-

quently groomed themselves during the trials, and none of them ate during the trials.

Aggressive Behavior.—Ten intraspecies aggression trials were conducted among the male *Microtus* and 19 among the male *Peromyscus*. The *Microtus* trials resulted in a total of 94 contact reactions, for an average of 4.7 contacts per trial. The *Peromyscus* trials resulted in 190 contact reactions for an average of five contacts per trial. Table IV gives the results of analysis of the contact reactions for both species.

The results of the intraspecies contests indicate that there was little aggressiveness between individuals of the same species. Only a negligible amount of fighting, aggressive, or recessive behavior was exhibited in these intraspecies trials. Dominance between two individuals was established primarily through grooming. The dominant individual groomed, and the recessive individual submitted to the grooming. The pair being tested frequently spent a good part of the period huddled together in a corner.

A total of 108 interspecies aggression tests were conducted, giving 1130 contact reactions, for an average of 5.23 contacts per trial. The average number of contacts per test was about the same for both the intraspecies and the interspecies trials. The analysis of contact reactions for these trials is also reported in Table IV. A comparison of the first three columns for both the intra- and interspecies tests immediately reveals a vast difference in the aggressive behavior of these two species. The figures listed in the first column of Table IV for the interspecies aggression study indicate which species started the fight. The *Microtus* appeared far more aggressive in this respect than the *Peromyscus*. The figures for aggressive behavior substantiate this idea, as does the large percentage of recessive behavior attributed to the *Peromyscus*. No difference for the two species can be noted from the last three columns.

The *Peromyscus* presented an over-all picture of recessiveness. They seldom resisted when the *Microtus* moved into their end of the cage, and removed food or nesting material. Their flight from the advance of a *Microtus* frequently took the form of frantic leaps, or cling-

Table IV.—Tabulation of the results of the aggression studies; figures represent the percent of contacts resulting in the categorized behavior for each species.

	Actual Fighting	Aggressive Behavior	Recessive Behavior	Fraternizing	Sniffing	No Reaction
INTRA						
Microtus	3.19	1.06	2.13	20.22	39.40	34.00
Peromyscus	0.00	0.53	1.05	38.42	21.58	38.42
INTER						
Microtus	79.3	84.6	4.1	45.40	53.20	54.50
Peromyscus	20.7	15.4	95.9	54.60	46.80	45.50

ing to the wire roof of the cage. If they did not flee the meadow mouse's advance they generally assumed the defensive stance, or crouched with eyes closed against the wall. They seldom made any noise in resisting attacks.

Aggressive behavior by the meadow mice was most commonly evidenced by charging and squeaking, directed at the white-footed mice. The meadow mice frequently chased the white-footed mice around the cage, squeaking, and nipping at their hind-quarters. Any assault by the white-footed mice was ignored by the meadow mice. No serious physical injury resulted from any of the fights.

DISCUSSION

The results of the artificial habitat study indicate a positive orientation of the meadow mouse to the broomsedge habitat. Pearson (1959) reports this type of orientation in the natural habitat in the same fields from which these animals were removed. The association has also been noted by Eadie (1953), who suggests that it is a response to the amount of vegetational cover.

The data do not, however, support the position of Pearson (1959) that the white-footed mouse is positively associated with the goldenrod-aster habitat. The fall and spring trapping indicate that the white-footed mouse is captured with less effort in the goldenrod-aster habitat, but in the present study there was no significant statistical association of captures with habitat. The studies in the simulated habitat showed that there may be no differential orientation in selection of habitat and there was no positive association in time spent with either of the habitats.

These artificial habitats were designed to emphasize orientation through visual clues provided by the gross form characteristic of the two microhabitats. However, these were only artificial habitats, and different associations might occur if more emphasis were placed on olfactory or tactile senses. It is difficult to ascertain exactly when and where discrimination actually took place. Perhaps the *Microtus* discriminated at the site of introduction to the habitat, and the simulated broomsedge satisfied the cover requirements of the species. In the orientation trials *Peromyscus* changed habitats twice as much as *Microtus*. This may indicate that *Peromyscus* did not discriminate at the time and point of introduction to the habitat, and/or, neither simulated habitat provided a satisfactory stimulus. Existence of either of the above conditions would produce random search behavior.

The conclusion drawn from the aggression studies is that the meadow mouse is definitely the more aggressive species. Meadow mice were responsible for starting 79 percent of all the fights observed, and they exhibited 85 percent of the recorded aggressive tendencies. The white-footed mice, by comparison, exhibited 96 percent of all recorded recessive activity. The recessivity of white-footed mice has been recorded by King (1957), whose study was on conflicts between house mice and deermice, *Peromyscus maniculatus*. A comparison of his re-

sults with those of the present study strengthens the conclusion that the white-footed mouse exhibited very few aggressive tendencies under these experimental conditions.

A significant decrease in population level is apparent upon comparison of the census data from Pearson (1959) with those of the present study. The levels in all but one case have shown a decrease of at least 40 percent, using Pearson's record of captures opposed to the record of the present study. In most cases where heavy *Microtus* activity had been observed two years earlier the runways were still present but little activity was noted. The runway maze was trapped, using the same traps and type of bait employed by Pearson, but few meadow mice were captured.

Consideration of the possible reasons for the change in population levels gives some clue as to why the association of white-footed mice to the goldenrod-aster habitat did not hold. The cyclic phenomenon of population fluctuation for small mammals has been studied by Hamilton (1940), Davis (1933), Christian (1950), Godfrey (1955), Jameson (1955), and others. *Microtus* have an approximate three- to four-year cycle, and Christian has advanced the theory that adreno-pituitary breakdown, resulting from stresses caused by overpopulation, plays an important role in the sudden increase in mortality. Only three female meadow mice were taken in the census, and two of them, plus six males, died within two months of capture. The deaths observed were accompanied by symptoms similar to those described by Christian of adreno-pituitary breakdown.

On the basis of these observations it appeared that the *Microtus* population in the area studied had recently passed the height of its cycle and had moved rapidly downward.

Pearson (1959) concluded that the white-footed mouse was associated with the goldenrod habitat, while the results of the present study indicate that the white-footed mouse is randomly oriented. The orientation for this species to habitats other than broomsedge which Pearson reported was probably due to: 1) the high level of the *Microtus* population, 2) the positive orientation of *Microtus* to the broomsedge habitat, and 3) the aggressive tendencies of *Microtus* experimentally suggested by this study. The increased number of captures of *Peromyscus* in the broomsedge habitat can probably be attributed to the low *Microtus* population level, and the subsequent lack of sufficient aggressive response by the meadow mouse to the entrance into the broomsedge of a larger number of white-footed mice.

An examination of the broomsedge habitat and the goldenrod-aster habitat reveals a great difference in the type and amount of cover provided. The former, with its dense mat of short grasses, lichens, and young plants, interspersed with large clumps of broomsedge, provides a continuous cover for runways and feeding activity. This may be another reason for the high utilization of the broomsedge habitat reported by the current census. The goldenrod-aster habitat has a low ground cover of annual and perennial herbs, not forming a continuous cover, and an upper layer of the stems and leaves of the forbs. The

broomsedge habitat provides year-round cover while the forb cover is largely destroyed during the winter, beaten down by rain and snow, leaving only underground burrows for shelter.

Additional information on the orientation of these two species will probably be obtained upon further study of their feeding habits. The meadow mouse may be restricted in its habitat association by its utilization of the shoots and leaves of plants. The white-footed mouse appears to feed chiefly upon trees and shrubs. Upon examination of the vegetation of most fields, it is apparent that the production of forbs and grasses is far more regular than the production of mast and fruit. The irregular pattern of tree and shrub growth, as compared to the extensive ground covering in the broomsedge habit makes it possible that the white-footed mouse is, of necessity, more widely oriented with regard to habitat. Hamilton (1937b) gives the meadow mouse a home range the size of a tennis court while Blair (1942) gives the male white-footed mouse a home range of around 2.31 acres. Food preference may, therefore, have an effect upon the habitat orientation in these two species.

SUMMARY

1. Although there was no statistical association between capture of meadow mice and the broomsedge habitat established by the census, the artificial habitat studies indicate that *Microtus* is positively oriented to the broomsedge habitat.

2. The artificial habitat studies indicate that *Peromyscus* is randomly oriented with regard to habitat, and the trapping data reveal that this species was captured in all major habitats. Though it was most prevalent in the goldenrod, there was again no statistical association between capture and goldenrod.

3. Studies of aggressive tendencies point out the fact that the meadow mouse is more aggressive than the white-footed mouse.

4. The occurrence of the white-footed mouse may be affected by the population level of the meadow mouse. The meadow mouse is positively oriented to the broomsedge habitat, it is more aggressive than the white-footed mouse, and when the population level is high for the meadow mouse few white-footed mice are found in the broomsedge habitat.

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The Taxonomic Status of Eleocharis elliptica

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During the course of an investigation of the Cyperaceae of Illinois, great difficulty has been encountered in determining some species of *Eleocharis.* Further study revealed many irregularities which exist in several species complexes. This paper is an attempt to show the relationships believed to exist in one of these complexes in Illinois.

In this study, 157 mature individual plants were examined. The authors wish to thank the curators of the following herbaria who kindly loaned specimens of *Eleocharis:* Chicago Museum of Natural History, Illinois State Museum, University of Illinois, Illinois Natural History Survey, Western Illinois University, and Eastern Illinois University.

Recent Taxonomic Status

The taxonomy of *Eleocharis tenuis, E. elliptica,* and *E. compressa* has been difficult and interpreted differently by various workers in the past. In Illinois, Jones (1950) and Jones, *et al.,* (1955) recognized *E. tenuis* and *E. compressa* while placing *E. elliptica* in synonymy with the former. Gleason (1952) likewise recognized *E. tenuis* and *E. compressa,* but following Svenson's proposal in 1932, relegated *E. elliptica* to varietal status under *E. tenuis,* as var. *borealis.* Fernald (1950) and Svenson (1957), the most recent monographer of the genus, maintain all three species as distinct, although Svenson states that *E. elliptica* and *E. compressa* may tend to intergrade at their range's limit.

Eleocharis tenuis has been divided into three varieties, with only var. *verrucosa* occurring in Illinois. The typical variety from the east coast and var. *pseudoptera* from the eastern states are excluded from this discussion.

The characteristics that are used usually to distinguish *E. tenuis* var. *verrucosa, E. elliptica,* and *E. compressa* follow:

E. tenuis (Willd.) Schultes var. *verrucosa* Svenson.—This taxon is characterized in most treatments as having culms 4- to 5-angled, a mucro at the tip of the truncate sheath, the lowest scale of the spikelet suborbicular, and the achene 0.8-1.0 mm long, olivaceous, warty, with a depressed tubercle ⅛ the length of the achene.

E. elliptica Kunth.—This species is usually described as having culms 6- to 8-angled, a short mucro at the tip of the truncate sheath, the lowest scale of the spikelet suborbicular, the achenes 1.0 mm long, yellow to dull orange, undulate, with a depressed tubercle with an apiculate center.

E. compressa Sull.—This species is traditionally characterized by its strongly flattened culms, its truncate sheath which is faintly to prominently toothed, and its achenes 1.0-1.5 mm long, golden-yellow

to brown, granular-roughened or reticulate, with a depressed or globose-conic tubercle.

Analysis of Characters

Culm angles.—In the past one of the best ways given for distinguishing these three taxa is on the shape of the culm. *Eleocharis tenuis* var. *verrucosa* is reported to have a 5-angled (rarely 4-) culm, *E. elliptica* a 6- to 8-angled culm, and *E. compressa* a merely flattened culm. Thorough study of the culms of these taxa shows that these differences are attributable to the number of vascular bundles present in the culms. Thus *E. tenuis* var. *verrucosa* always has 4 or 5 bundles per culm, thereby accounting for the 4- to 5-angled culm. When 5 bundles are present, the culm has a pentagonal shape. (For illustrations, refer to Svenson, 1932.) *E. elliptica* has been described as having culms with 6-8 angles. The angled appearance is due to the presence of 6-8 vascular bundles. (One exception was a non-angled specimen with 6 vascular bundles.) In some instances the angled appearance of culms with 6 to 8 vascular bundles may be due to desiccation from preserving; the tissue opposite the bundles protrudes inward. The angles of these culms are less pronounced than the angles of *E. tenuis* var. *verrucosa*. *E. compressa* has been described as having compressed culms. Those specimens with compressed culms possess 9-14 vascular bundles. In most instances the culms did not appear to be prominently angled due to the more or less bilateral arrangement of the bundles which give the culms a flattened appearance. The width of the culm, correlated with vascular bundles per culm, is tabulated in the following table. Some overlapping of culm width does occur.

Vascular Bundles	Average Culm Width
5	0.3-0.6 mm
6-8	0.4-1.1 mm
9-14	0.9-1.5 mm

Tip of sheath.—All three entities bear truncate sheaths, with short mucros attributed to *E. tenuis* var. *verrucosa* and *E. elliptica*. *E. compressa* is said to have a toothed sheath apex. Our study finds that while mucros are generally present in *E. tenuis* var. *verrucosa* and *E. elliptica,* there are some specimens in which a mucro is lacking. *E. compressa* is usually truncate without a mucro; however, in a few specimens a mucro is present. Because of the spasmodic occurrence of the mucro, little significance can be given to this character.

Lowest sterile scale of spikelet.—The lowest scale of the spikelet in *E. tenuis* var. *verrucosa* and *E. elliptica* is said to be suborbicular. No mention is ever made of the lowest scale in *E. compressa.*

A study of the Illinois material shows that *E. tenuis* var. *verrucosa* and *E. elliptica* always have a lower scale that is suborbicular and completely encircling the culm. Ninety-eight percent of the E. *compressa*

examined have the same type of lower scale. No taxonomic value may be given to this character because of its presence in all three taxa.

Fertile scales.—The fertile scales of Illinois *E. tenuis* var. *verrucosa* are ovate, obtuse or acute, dark purple or black with a light green midrib. The fertile scales of Illinois *E. elliptica* and *E. compressa* are almost identical, both having fertile scales ovate to lanceolate, obtuse to acute, with varying color. The scales of *E. compressa* were usually slightly larger, and the tips of the scales were more commonly bifid in *E. compressa* than in *E. elliptica*.

Achene size.—Achenes range in length (minus the tubercle) from 0.6 mm to 1.2 mm. Specimens with 5 vascular bundles per culm (*E. tenuis* var. *verrucosa*) have slightly smaller achenes. Those with 6-14 vascular bundles per culm (*E. elliptica* and *E. compressa*) have similar sized achenes (0.8-1.2 mm long, 0.6-0.9 mm) wide. On this basis no distinction is possible between *E. elliptica* and *E. compressa*.

Achene color.—Another character usually considered useful in separating the three taxa is achene color. Achenes of *E. tenuis* var. *verrucosa* are said to be olivaceous, *E. elliptica* to be yellow to dull orange, and *E. compressa* to be golden-yellow to brown. By reference to Ridgway (1912), the mature achenes of the Illinois material could be divided into 24 technical colors. Since many of these colors are very close to each other and because such a large number is difficult to work with, the 24 colors were subdivided into four "basic color" groups. These four, along with their included technical colors, are as follows:

Orange Brown—Mars Yellow, Raw Sienna, Tawny.

Yellow—Empire Yellow, Light Cadmium, Aniline Yellow, Yellow Ocher, Olive Yellow, Cream Buff, Reed Yellow, Honey Yellow.

Olive—Sulphine Yellow, Ecru Olive, Light Yellowish Olive, Yellowish Olive, Dark Greenish Olive.

Brown—Ochraceous Tawny, Buckthorn Brown, Dresden Brown, Mummy Brown, Old Gold, Isabella Color, Tawny Olive, Saccardo's Umber.

The achene color is exceedingly variable. Many specimens have two or sometimes three basic color types of achenes. Of the four basic groups of color, yellow is present in all three taxa. Brown is common in specimens usually referred to *E. elliptica* and *E. compressa* while it is almost completely lacking in *E. tenuis* var. *verrucosa*. Olive is found almost exclusively in those specimens called *E. tenuis* var. *verrucosa*. Aside from the normal yellow color sometimes found in *E. tenuis* var. *verrucosa,* a dull yellow color could be induced on some of the mature olive achenes by scraping off the outermost cell wall layer. Orange brown is common in *E. compressa,* occasional in *E. elliptica,* and completely absent in *E. tenuis* var. *verrucosa*. In most instances color may

be used to segregate most specimens of *E. tenuis* var. *verrucosa* from specimens of *E. elliptica* and *E. compressa,* but color cannot be used to segregate *E. elliptica* from *E. compressa.*

Shape of tubercle.—The study of Illinois material reveals that the tubercles in all three taxa may be conical, depressed, or depressed with an apiculate center. All types may be found occasionally on the same plant.

Size of tubercle.—Width measurements of the tubercle were taken on all specimens that had 6 or more vascular bundles. Specimens with 6-8 bundles have on the average slightly wider tubercles (0.4 mm) than those with 9-14 bundles (0.3 mm wide). The height of the tubercles was variable in both groups.

SUMMARY AND CONCLUSIONS

1. Whether the culm is angled or compressed depends upon the number of vascular bundles present. In general, the three taxa fall into three different groups.

2. The tip of the sheath and the shape of the lowest scale of the spikelet are nearly constant in the three taxa.

3. The fertile scales of *E. tenuis* var. *verrucosa* are generally distinct from the other two taxa, being smaller and darker in color than the scales of *E. elliptica* and *E. compressa.* The scales of *E. compressa* may at times be somewhat larger than those of *E. elliptica.*

4. The achenes of *E. tenuis* var. *verrucosa* are in general smaller than the achenes of the other two taxa. *E. compressa* and *E. elliptica* achenes are about the same size.

5. Color of achenes is exceedingly variable, but olivaceous achenes almost always indicate *E. tenuis* var. *verrucosa.* The other taxa are indistinguishable on achene color.

6. *E. tenuis* var. *verrucosa* nearly always has warty achenes; *E. elliptica* and *E. compressa* are virtually indistinguishable on achene texture; however, many *E. elliptica* achenes may appear to be slightly warty or undulate, whereas all *E. compressa* achenes are reticulate.

7. The shape of the tubercle is too variable among the three taxa to have any taxonomic significance.

8. *E. elliptica* seems to have a slightly wider tubercle than *E. compressa.*

9. It seems best to treat *Eleocharis tenuis* var. *verrucosa* as distinct from *Eleocharis compressa* and to make *E. elliptica* a variety under *E. compressa.* For this latter transfer, the following combination must be made:

Eleocharis compressa Sull. var. **borealis** (Svenson), comb. nov.

Eleocharis elliptica Kunth, Enum. Pl. 2:146. 1837.
Eleocharis capitata var. *borealis* Svenson, Rhodora 34:200. 1932.

A KEY TO THE COMPLEX OF ILLINOIS ELEOCHARIS TENUIS

A. Culm with 5 vascular bundles and appearing 5-angled; mature achene usually olivaceous, warty, 0.6-0.9 mm long (excluding the tubercle) .... *E. tenuis* var. *verrucosa*

A. Culm with 6-14 vascular bundles and appearing with low angles or compressed; achene usually yellow, brown, or orange-brown, reticulate or slightly warty, 0.8-1.2 mm long (excluding the tubercle).

B. Culm with 6-8 vascular bundles and appearing with 6-8 low angles; achenes slightly warty or reticulate ....*E. compressa* var. *borealis*

B. Culm with 9-14 vascular bundles and appearing compressed; achenes reticulate ....*E. compressa* var. *compressa*

ABERRANT INDIVIDUALS

To avoid confusion 3 specimens were not used in the previous study. A brief description of these follows:

Hatcher 147, SIU.—Culms with 4 vascular bundles; achenes 1.1 mm long, 0.7 mm wide, brown, reticulate; tubercle depressed, 0.5 mm wide.

William Hardy 9, SIU.—Culms with 4 vascular bundles; achenes 1.0 mm long, 0.8 mm wide, brown, reticulate; tubercle depressed, 0.5 mm wide.

William Hardy 9, SIU.—Culms with 5 vascular bundles; achenes 1.0 mm long, 0.8 mm wide, brown, reticulate; tubercle depressed, 0.5 mm wide.

The above specimens were collected at the same area on the same date. Unfortunately the whole plants could not be observed as the two herbarium sheets that these specimens were mounted on were composed of loose aggregations of culms.

Hatcher 147 (culm with 4 vascular bundles) was with a specimen that had a culm with 6 vascular bundles, achenes 1.1 mm long, 0.8 mm wide, brown, reticulate, and the tubercle depressed and 0.5 mm wide.

The achenes of the above specimens looked identical, and the various culms of these specimens may actually be from the same plant, thus leading to greater confusion within the group. The significance of these plants is at the present time unknown, thus meriting further investigation.

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The Maintenance of the Sternal Egg Sac Position by Pisaurid Spiders

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Nursery web spiders (Pisauridae) have as their closest known relatives the wolf spiders of the family Lycosidae (Bishop, 1924). Among the differences used to separate these two taxa are the conformation of the egg sac and the manner in which the female spider carries the sac. The pisaurid egg mass is enclosed in a continuous covering of silk and is held beneath the female's sternum by the chelicerae. The lycosid egg sac is composed of two valves. It is attached with webbing and swung below the mother's spinnerets. Gertsch (1949) mentioned that the sternal egg sac position is more ancient and awkward than the abdominal position. The purpose of this paper is to suggest a reason for the maintenance of the sternal egg sac position by pisaurid spiders.

McAlister (1959) pointed out that the ability to dive beneath the water is an escape mechanism important to the survival of *Dolomedes triton sexpunctatus* Hentz. This is probably true for the other species of diving pisaurids. It can be explained that if the ability to dive successfully is an asset to these spiders, then the sternal egg sac position is also advantageous, for it facilitates the diving process more than would the abdominal position.

An adult female *D. t. sexpunctatus* weighing 1.50 gm. (equivalent to 1470 dynes) displaced 1.53 gm (1499 dynes) of water when completely immersed. When this individual is submerged there is a buoyant force of 1499 dynes tending to push her to the surface. The spider must therefore exert a force of 29 dynes upon some support to remain underwater (Fig. 1A). This specimen carried a spherical egg sac 1.6 cm in diameter which had a mass of 2.10 gm (2058 dynes). Assuming the sac to be a perfect sphere, its volume was calculated at 2.15 cc. The buoyant force on the sac will be equivalent to the weight of the water which it displaces (= sac volume) or 2.15 gm (2107 dynes). Figure 1B indicates that a downward force of 49 dynes must be provided by the spider to keep her egg mass from bobbing to the surface. The female spider must overcome a net unbalanced force of 78 dynes to remain submerged with her burden. It is important to note that the larger buoyant force vector, that acting on the egg sac, is directly beneath the spider's body where it can be most easily balanced by the tension force of the ambulatory legs (Fig 1C). If the egg sac were posteriorly located it would tend to raise the hind end of the spider, or at least to unbalance her.

The force which a spider must exert to remain submerged is small compared to that which is required for it to break the surface film. An individual *D. t. sexpunctatus* with a mass of 0.447 gm (438 dynes)

fell through the surface film of water when the surface tension was reduced to 38.8 dynes/cm. These figures can be substituted into the formula $St = \frac{Wt^*}{2L}$ to compute the effective contact line between the animal and the surface film (in this case 11.3 cm). This contact line computation can be used as a constant, if the same individual

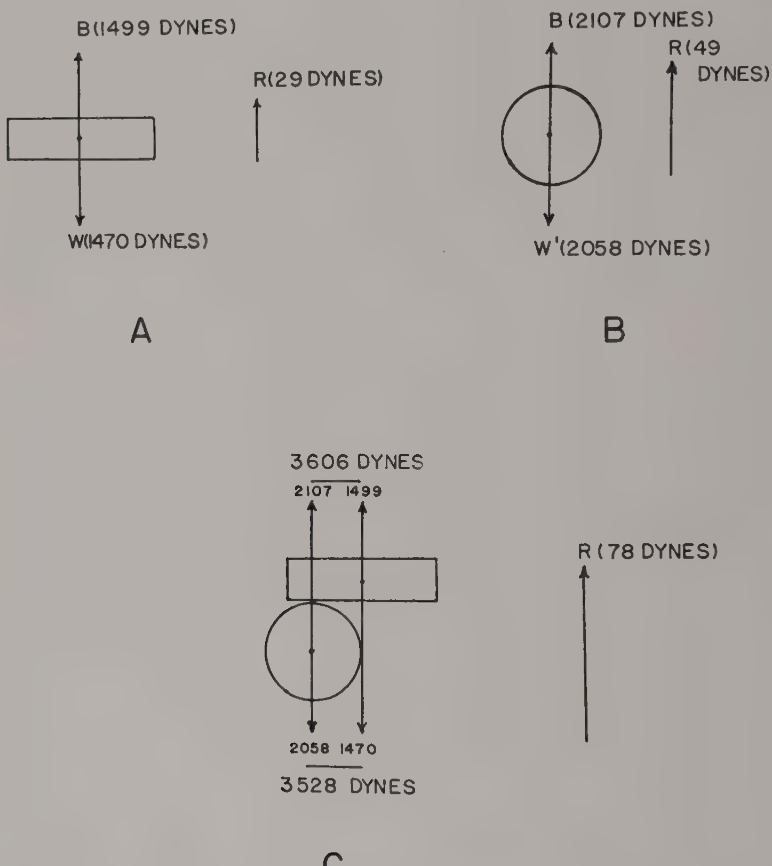

Fig. 1.—Diagrammatic representation of force vectors involved in the diving and submersed activities of the spider, *D. t. sexpunctatus* (rectangle), with its egg mass (circle). Abbreviations are as follows: B—buoyant force; W—weight of spider; W′—weight of egg sac; R—unbalanced force.

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* St is the surface tension in dynes/cm; Wt is the weight of the animal in dynes; 2L is the line of contact between the organism and the surface film, in centimeters.

spider is concerned, to determine that in pond water (St =65 dynes/cm) a force of 735 dynes must be created for this specimen to break the surface film. When the egg sac mentioned above is considered, the known diameter (1.6 cm) can be used to figure the contact line, which will be equivalent to the egg sac circumference ($C = 2\pi r = 5.03$ cm). In pond water at a surface tension of 65 dynes/cm a force of 327 dynes is required to push the egg sac through the surface film. The spider must therefore provide a momentary force of 1062 dynes (or 1.08 gm) when she breaks the surface film of pond water with her egg sac.

McAlister (1959) stated that *D. t. sexpunctatus* enters and emerges from the water head first. Females of this species were observed to dive in this manner with their egg sacs in the San Marcos River, Hays County, Texas. The sternal egg sac position may be related to the diving behavior in either of two ways: a) if the egg sac was sternally carried before the diving behavior developed, the head first manner of breaking the surface film may have become established because it is easier for the spider to overcome relatively large surface film and buoyant forces if the egg sac is directly beneath the body; b) if the habit of diving was developing while the egg sac was carried beneath the spinnerets the movement of the egg mass to the chelicerae may have occurred because it facilitated the diving process and the maintenance of a submerged position. In the first case the egg sac position is a contributory cause, and in the second case a result of the head-first manner of diving. Since Gertsch (1949) considers that the anterior egg sac position antidated the abdominal position, perhaps the first of the above alternatives is the correct one.

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Innate and Environmental Dispersal of Individual Vertebrates

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Little is known about the rates of dispersal of the young of wild populations of vertebrates, because it is difficult to recover marked individuals after they have dispersed to breed elsewhere. Nevertheless, growing evidence suggests that the observed dispersal patterns may be governed by the laws of heredity as well as being influenced by population pressure.

Dispersal of an individual vertebrate is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate. The significant role of an individual's dispersal is the greatest distance its genetic characteristics are transmitted, rather than the greatest distance the animal may have migrated or otherwise traveled away from the place where it was conceived, hatched or born. Most, but not all vertebrate animals make some sort of a dispersal movement at about the time they attain puberty, regardless of their actual age. Individuals that make innate dispersals, as defined by the hypothesis advanced herein, are predisposed at birth to disperse beyond the confines of their parental home range. They ignore available and suitable niches and voluntarily disperse into strange and sometimes even unfavorable habitats (Fig. 1). In contrast, environmental dispersal is defined as the movement an animal makes away from its birthplace in response to crowded conditions (mate selection, territoriality, lack of suitable homesites, or parental ejection). Environmental dispersers are assumed to have inherited a homing tendency. Environmental dispersal is a density-dependent factor, whereas innate dispersal is independent of density, but both are presumed to be inherited traits.

Even though the hypothesis that vertebrates are predisposed at birth to make either innate or environmental dispersal movements still needs to be substantiated, it seems worth while and desirable to present this concept at this time as a stimulus to further research on this neglected aspect of population ecology. In the literature there are many statements implying that vertebrates disperse because of population pressure factors, but there are relatively few that support the innate dispersal hypothesis.

Burt (1949) wrote, in regard to rodents and other mammals, "If . . . there is an inherent desire to wander, it most certainly is not developed to the same degree in all individuals of a species." Blair (1953) theorized that the dispersal of rodents may result from either population pressure or "an inherent tendency to disperse, stimulated by physiologic changes as the animal becomes sexually active." Dice

and Howard (1951) provide some support for an innate and an environmental dispersal trait, for they found that dispersal distances of prairie deermice (*Peromyscus maniculatus*) are nonrandom — that apparently there is an innate stimulus which might motivate certain individuals but not others to leave the vicinity of their birthplaces. Johnston (1956) similarly found that salt-marsh song sparrows did not have a random dispersal pattern. As with the deermice, too many birds aggregated close by, too few moved intermediate distance (350 to 650 meters), and too many moved beyond 650 meters. He says that both his data and those of Mrs. Nice (Ohio song sparrow) have dispersal curves that differ from the expected significantly at the one percent level.

In an intensive study of valley quail by Howard and Emlen (1942), the birds were marked individually with colored bands, and practically every bird in three of six coveys studied was readily observed each day from an automobile. In this quail population there was an interchange of a few members between coveys prior to the spring nesting. At this time, additional, unmarked birds appeared from more distant coveys, and some resident birds disappeared. In every case when a strange bird attempted to merge with a new covey, it was repeatedly attacked for about a month, and ostracized by the members of the same sex in the covey. These ostracized birds had not been driven from their original coveys; they left voluntarily, and patiently awaited acceptance into a different covey. At that time of the year the birds were pairing,

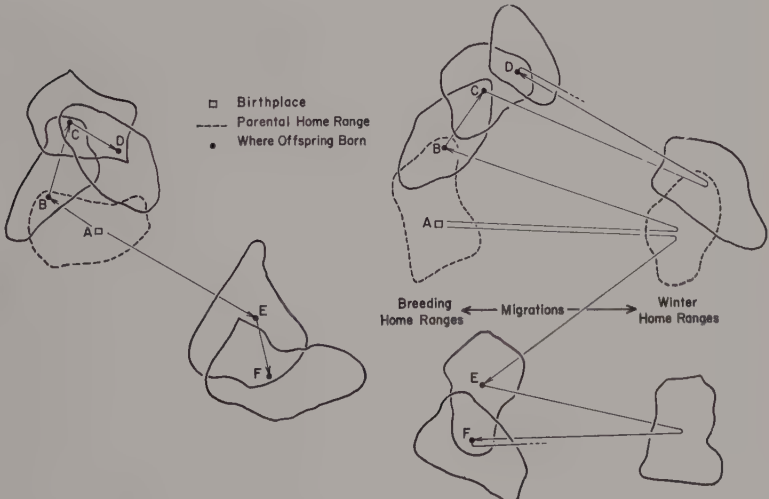

Fig. 1.—A schematic drawing illustrating distance of innate dispersal movements (shortest line between A-E) and of environmental dispersal changes of home ranges (the shortest distance between A-B, B-C, C-D, and E-F) for nonmigratory (left) and migratory (right) animals.

although still in covey formation. Individuals of both sexes made dispersal movements, even though there were unpaired members of the opposite sex in the coveys they left. Perhaps "shuffling" in bobwhite quail is a similar phenomenon and is also composed of innate dispersers.

Von Haartman (1951) made a study in Finland of the tendency of pied flycatchers to return to their birthplaces. According to a review of von Haartman's article by Huntington (1951), about three times as many young females as young males did not return to their birthplaces. Many of these probably made innate dispersals. Of the birds that returned the second and following years after banding, the percentage was about the same for both sexes. Von Haartman considers the homing, or philopatric, quality to be hereditary rather than due to greater success in competition for territory, because combat is unusual in the females, and unsuccessful attempts to settle were much more common in males than in females. Furthermore, the dates of arrival and egg-laying of philopatric females were not significantly earlier than those of others. Apparently the nonphilopatric adult females lack a genetically controlled factor that makes their home-loving sisters try to settle in a familiar place. If that is so, then the nonphilopatric individuals may likewise possess a genetically controlled factor for innate dispersal. Of course, innate dispersal and philopatry may not be the hereditary consequence of each other, but von Haartman does consider the differences, *i.e.,* the variation in dispersal distance, to be inherited. He suggests that philopatry may be a recessive character, because six (3%) offspring of 196 banded philopatric females returned to the area, whereas only three (0.5%) offspring of 632 nonphilopatric females returned. This information is too meager to permit drawing any definite conclusions, but it provides some support for the hypothesis that philopatry, hence, also innate and environmental dispersal, are genetically determined.

There are numerous examples indicating that a certain percentage of both males and females (it will vary with species) is likely to make extensive dispersal movements. Only one case will be cited here. In Fitch's (1948) careful investigation of ground squirrels on an 80-acre plot, he found that 40.9 percent of young females survived to maturity, whereas only 31.1 percent of the males survived. He attributes this difference to an "extensive movement of young males off the area rather than actual mortality."

Introduced animals, like the English sparrow and starling in North America and rabbits in Australia and New Zealand, spread their range far more rapidly than population pressure factors could have demanded. It seems more likely that certain young individuals inherit an instinct to disperse considerable distances, and that is why the range of introduced species is often greatly extended by the time the earlier occupied habitats become crowded.

In 1905, three female and two male muskrats were released in two small natural ponds in Dobrisch, 40 km southwest of Prague.

Nine years later the resulting population in Bohemia was estimated at two million (Mohr, 1933). It takes very little calculation to realize that such a large population could not have resulted if young muskrats had not dispersed until population pressure in each favorable habitat caused them to disperse to the next available homesite. On the contrary, as the result of the presumed innate dispersal urge, there must have been a rapid spreading of individuals into new areas long before the populations they left behind had become very large. By the time the populations in the earlier occupied habitats approached overcrowding, which also probably resulted in increased mortality and decreased fecundity, the range of the species had probably already been extended many miles.

Beer and Meyer (1951) report on muskrats as follows: "The bulk of the reports on movements in the Madison area are received in March with a few in February and quite a few in April. This agrees with the period of increasing gonadotropic activity of the pituitary and the rapid development of the gonads. We believe that these early spring movements may be induced by an increased irritability of the animals or to an urge within the animal to move and that the latter is probably the closest to being correct, since the animals found in the early part of the spring movement have few, if any, wounds from fighting. The group that is found moving from April through July are usually severely wounded from fighting. These movements should be classified as force-out movements induced by population pressures."

Davenport (1915) stated that the nomadic impulse in man is an instinct that is sex-linked. Even though there seems to be little doubt that the dispersal trait is subject to the laws of heredity, additional evidence is necessary before one can be certain that the innate dispersal impulse is sex-linked, sex-modified, recessive, polygenic, or just how it operates.

At the San Joaquin Experimental Range, California, the author captured dispersing rodents in seven funnel traps located along drift fences of hardware cloth (patterned after traps used by Imler, 1945). With the nine species of rodents concerned, results indicate that the dispersal trait might be sex-linked, for about two males were captured for each female. Out of 766 trapped individuals that were carefully sexed, an average of 63 percent were males. It is interesting to note how close all these species independently approached this average. The percentage of male rodents captured between June, 1949, and July, 1952, is as follows (total number of individuals appears in parentheses): *Citellus beecheyi* 71% (7 individuals); *Thomomys bottae* 62% (158); *Perognathus inornatus* 68% (71); *Dipodomys heermanni* 61% (18); *Reithrodontomys megalotis* 63% (65); *Peromyscus maniculatus* 63% (51); *Peromyscus boylei* and *P. truei* 62% (26); and *Microtus californicus* 63% (370). If no locally established rodents or environmental dispersers had been captured, the figure might have been even closer to two males for each female. The traps were examined almost daily for four years and, at that time, it was obvious that nearly all the individuals captured were virgins in the act of dispersing.

In an attempt to measure the degree of dispersal among prairie deermice (*Peromyscus maniculatus*) living on 300 acres of grassland, the birthplace, distance of dispersal, and subsequent breeding site were learned for 155 (77 males and 78 females) of the young deermice (Howard, 1949). An arbitrary figure of 500 feet, which is beyond the boundary of most parental home ranges, is used to separate innate dispersal from environmental dispersal.

The over-all pattern of dispersal observed in the deermice seemed to indicate that: 1) the availability of surplus home sites (at least artificial ones) had little influence on degree of dispersal; 2) virgin mice made their extensive dispersal, if they ever made one, when they attained puberty, regardless of whether at 4.5 weeks or 25 weeks old (reflecting the season when born); 3) even though various proportions of the sexes were found in the same nest during the breeding season (up to two pairs were present together in the same nest boxes), there was no tendency for deermice to aggregate in the presumably more favorable habitats; 4) there was apparently very little trial and error searching for suitable niches, for dispersers were never found at intermediate points, suggesting that the dispersal urge for each individual was satisfied in a day or two; 5) individuals did not make more than one extensive dispersal, even if they later lost their mate, although there were minor shifts of nest sites, usually with each new

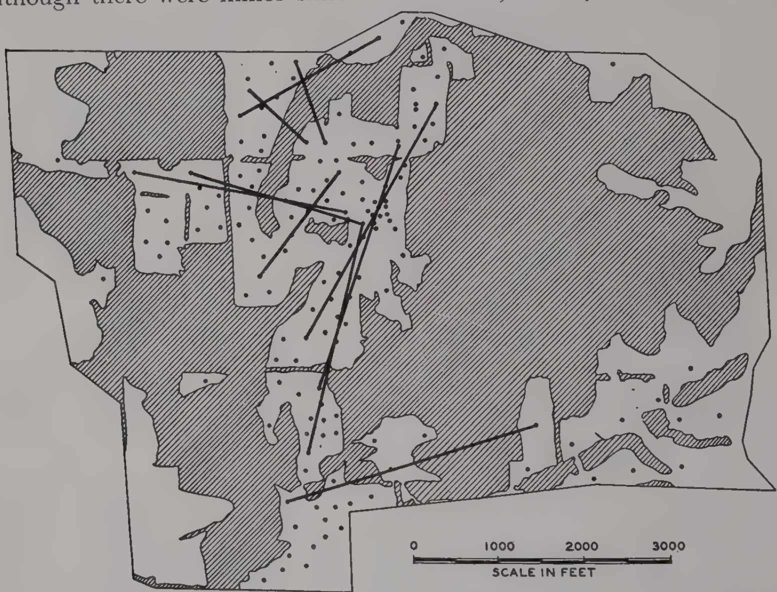

Fig. 2.—The lines indicate ten examples of extensive, innate dispersal movements made by prairie deermice on the Edwin S. George Reserve, Michigan. The grassland areas are unshaded and locations of nest boxes buried in field are marked by dots. (From Howard, 1949.)

litter; 6) when no suitable mates were present, some dispersers remained unmated for several months during the breeding season without moving, and adults did not move whenever an uneven sex ratio developed; and 7) there was no evidence suggesting that the parents forced the young to disperse, for quite frequently the mother would merely abandon the young and seek a new nest when a new litter was due.

With regard to the 36 deermice (out of the 155 that survived to breed) that made "innate" dispersals of 550 to 3300 feet into unfamiliar territory (Fig. 2), the following deductions have been drawn: 1) twenty-four (31%) of the males and 12 (15%) of the females made the extensive dispersals; 2) some individuals traveled through unfavorable habitats (woodland) even though their home range areas were largely surrounded by favorable grasslands; 3) only one animal (a male) was known to return to its birthplace a short time after dispersing (2050 feet); and 4) mice that dispersed the greatest distance did not have time to explore the areas adjacent to their birthplaces or the availability of the habitats through which they passed.

Discussion

If we assume that an innate dispersal trait exists, we can speculate on how the trait may be of value to a species: 1) it would bring about wide outbreeding; 2) it would help reduce the likelihood of too close inbreeding; 3) it would further the spread of new genes; 4) it would rapidly extend the range of the species as favorable habitats become available; 5) it would enable a species to reinvade areas depopulated by catastrophes, such as disease, fire, flood, abnormal weather, or man's activities, without having to start repopulating just at the edges and gradually overflow inward; 6) it would tend to reduce intraspecific conflict and bring about a more efficient utilization of habitat resources; and 7) it might spread a reservoir of characters of possible future value (not adaptive in the new situation yet not selected against, which might help explain why closely related species often differ by characters that are not adaptive).

Domestication probably favors the "homing" or environmental dispersal trait. If such is the case, domesticated animals introduced and released in foreign lands should spread their range more slowly than would be the case with their undomesticated relatives. There is some evidence that this is what happened with many of the introductions in New Zealand and with rabbits in Australia. Perhaps "wildness" is related to the adolescent wanderlust resulting from inheritance of the innate dispersal trait.

For the well-being of migratory species it is not only necessary that some individuals make extensive innate dispersal movements, but it is equally important that all other individuals return to the vicinity where raised. What would happen if most individuals of migratory populations did not tend to return to the home range? Chaos would

develop, for every individual would then be expected to return to the more preferred habitats in the breeding range of the species. There would be so much time and energy spent in establishing individual breeding territories that only a fraction of the total population would be able to breed, if the local food supply were not completely exhausted first. As it is, when the entire breeding range of a migratory bird, fish, or mammal is taken into consideration, there is a far more orderly establishment of the individual breeding ranges and territories than could possibly happen by chance, and natural selection has probably been important in the evolution of this pattern. Territoriality and environmental dispersals are of local importance rather than of geographic significance.

Since such a high proportion of the individuals making up mass emigrations are juveniles (Lack, 1954), it seems highly possible that they may also be responding to the innate dispersal trait. The higher the population density, the greater the number of innate dispersers. Such animals often pass up areas of abundant food supply, and the movements sometimes actually begin before there is any shortage of food. It seems possible that some emigrations, such as an occasional influx of snowy owls into northeastern United States, are merely an increased number of innate dispersers, brought about by an increase in population density rather than by an extensive shift in the home range of older adults. The age of this type of disperser needs to be determined to see if there are any old adults included, *i.e.*, individuals that have bred at least once before making the extensive dispersal. We also need to know if the distance of dispersal is any greater when population density is high.

If animals freely disperse in response to population pressure, then localized epidemics, or "outbreaks," should not occur. On the other hand, even though the direction of dispersal is probably inherently random, the direction of actual dispersal movements are probably greatly modified by many environmental factors. Consequently, there would be a greater tendency—for environmental dispersal movements in particular — toward the more densely populated regions of a species' range, where the more preferred habitats are to be found.

Howell (1922) put many of the factors to be considered in the dispersal of life into chart form. It seems quite plausible that the trigger mechanism initiating dispersals in many vertebrates is associated with the maturing of sex organs, as metabolic processes are speeded up by the activity of reproductive hormones. Lashley (1938) said that the "evidence points to the conclusion that the neural mechanism is already laid down before the action of the hormone, and that the latter is only an activator, increasing the excitability of a mechanism already present." Slonaker (1924 and 1927) recorded the rate of activity of albino rats in a revolving wheel, and noted that there was a marked increase in voluntary activity for males at puberty and for females during each estrus. It would be interesting to see if individuals

possessing the presumed innate dispersal trait had larger adrenals than the environmental dispersers.

Instinctive behavior does not necessarily have to be advantageous to the individual in a social species, but rather it may benefit the group by serving to maintain and spread the species (Tinbergen, 1951: 157). And, as pointed out by Tinbergen, homologous behavior elements may shift their position within the pattern and come to serve different functions in different species, or in some species become lost completely.

Many basic phenomena of animal behavior are not well understood, because they are difficult to investigate. It is particularly hard to analyze the inheritance of behavior patterns. The phenomenon of dispersal alone is a broad subject that will require the participation of many investigators. Much more information is needed about 1) the frequency with which different kinds of animals disperse various distances with population density at different levels; 2) the randomness of the distances of dispersal; 3) the sex ratio of the animals making extensive dispersals in relation to the current sex ratio of the local population; 4) the time relationships of the movements, and whether dispersals are always made at puberty; 5) the motivating and terminating forces, whether physiological or ecological; and 6) the genetic explanations of the variability observed in dispersal distances (field and laboratory experiments). Even if the innate concept should prove to be sound, much information will still be required to learn the various ways in which this behavior is expressed in different animal populations under different situations.

SUMMARY

Dispersal is the movement an organism makes away from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate. For the most part, the major dispersal movements are made by virgins about the time they attain puberty.

Possession of the innate dispersal trait implies that such an animal is predisposed at birth to leave home at puberty and make one dispersal into surroundings beyond the confines of its parental home range. Such density-independent individuals have inherited an urge to leave home voluntarily. They often pass up available and suitable niches and venture into unfavorable habitats.

Animals that make an innate dispersal movement are obsessed with a dispersal instinct. The "purposiveness" of the innate concept is not for the individual's welfare; rather, in spite of the high rate of mortality of innate dispersers, it has distinct survival value for the species. Innate dispersers are particularly important to a species because they, 1) increase the spread of new genes, 2) create wide outbreeding, 3) enable a species to spread its range rapidly as favorable habitats are created, 4) permit the species to have a discontinuous distribution,

and 5) help the species quickly reinvade areas that may have been depopulated by catastrophes, such as floods, fires, or man's activities.

Points that appear more or less to favor the existence of an innate dispersal concept include: 1) the distances of dispersal are, at least sometimes, significantly not random; 2) some introduced species spread their range too rapidly to be the result of population pressure factors; 3) reinvasion of a depopulated area does not commence at the edge and gradually overflow inward, but, instead, the density of the species builds up almost simultaneously over all of the area that is within the maximum limits of innate dispersals; 4) the rate at which innate dispersals are made seems to be density-independent; 5) the movements are made instinctively without any prior experience or instructors to imitate; 6) innate dispersers frequently cross or attempt to cross regions of unfavorable habitat, regardless of the availability of adjacent suitable habitats; and 7) the stimulus is of short duration, apparently being expressed only once, when the animal becomes sexually active for the first time.

The presence of the environmental dispersal trait implies that the individual will remain where born or, by means of trial and error, eventually select a new home range usually within the confines of its parental home range. It will have a strong homing tendency and move only as far as forced by population pressure factors (intraspecific competition or density-dependent factors) such as parental ejection of young, voluntary avoidance of crowded areas, mating and territoriality, availability of food and homesites, or the presence of other organisms including predators. Minor shifts of homesites result in a dispersal, but these are all called environmental dispersals, even though a series of them by one individual might eventually result in a total dispersal distance that is quite extensive, even exceeding that of some innate dispersal movements. Environmental dispersal has only local significance, whereas innate dispersal is of geographic importance.

To verify or refute the existence of an innate dispersal trait, the assistance of other investigators is urgently solicited, for findings of many workers will be necessary before we can thoroughly understand the dispersal behaviorism and dispersal pattern in different species.

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Studies on the Trematode Family Brachycoeliidae III. The Subfamilies Subordinate to the Brachycoeliidae and the Status of the Genus *Cymatocarpus* Looss, 1899[1]

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In Part I of this series of studies on the trematode family Brachycoeliidae (Cheng, 1958) was given an annotated list of the recognized species of *Brachycoelium* and in the same paper *Brachycoelium* was considered a member of the subfamily Brachycoeliinae under the Dicrocoeliidae; however, in Part II (Cheng, 1959), Brachycoeliinae was elevated to familial rank, following the suggestion of Johnston (1912). The decision to elevate this taxon to familial rank was based on newer information contributed by the discovery of the life cycle of *Brachycoelium obesum* Nicoll, 1914 considered elsewhere. Dispite the elevation of Brachycoeliinae to familial rank, the authors have seen fit to retain Looss' subfamily, Brachycoeliinae, to include the genera *Brachycoelium* and *Cymatocarpus* since these two groups are sufficiently different from the other genera included in the Brachycoeliidae to warrant their being placed in an independent subfamily.

Several other subfamilies have been erected in the past by various workers to receive several of the genera now generally considered to be related to the brachycoeliids. The validity and usefulness of some of these are questionable. Baer (1924) erected Cymatocarpinae to receive *Cymatocarpus;* Dollfus (1937) erected Orchidasmatinae for *Orchidasma,* a genus which cannot be justified as a member of the Brachycoeliidae although it had been considered by some as a close relative of the Brachycoeline Group; Dollfus (1929) erected Mesocoeliinae to receive *Mesocoelium;* and Dayal (1938) erected Leptophallinae for *Leptophallus.* Of these subfamilies, the first two mentioned possess no systematic significance and their deletion is therefore advocated. Cheng (1959) stated that the genera *Glypthelmins, Margeana* and *Reynoldstrema* should be assigned to the Glypthelminae Cheng, 1959, since these three genera are again sufficiently different from the other members of the Brachycoeliidae to warrant their assignment to the same subfamily. In order to clarify what the authors consider a natural systematic classification, the following taxonomic design is proposed and is being used throughout this study.

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[1] A contribution from the Department of Biology, Lafayette College and contribution No. 31-C from the Department of Histology and Embryology, Dental School, University of Maryland. This research was made possible by the National Science Foundation Award (Grant-2086) to the senior author, summer, 1958, Mountain Lake Biological Station, University of Virginia.

TAXONOMY OF THE BRACHYCOELIIDAE

Superfamily Dicrocoelioidea Faust, 1929
Family Brachycoeliidae Johnston, 1912
Subfamily Brachycoeliinae Looss, 1899
Genera *Brachycoelium* (Dujardin, 1845) Stiles and Hassall, 1898
Cymatocarpus Braun, 1901
Subfamily Leptophallinae Dayal, 1938
Genus *Leptophallus* Lühe, 1909
Subfamily Glypthelminae Cheng, 1959
Genera *Glypthelmins* Staffod, 1905
Margeana Cort, 1919
Reynoldstrema Cheng, 1959
Subfamily Mesocoeliinae Dollfus, 1929
Genus *Mesocoelium* Odhner, 1911

Cheng (1959) gave the definition of the subfamily Glypthelminae. It is felt that redefinitions of the subfamilies Brachycoeliinae Looss, 1899, Leptophallinae Dayal, 1938 and Mesocoeliinae Dollfus, 1939 are valuable in presenting the phylogenetic relationships within the Brachycoeliidae, hence these are given, incorporating the more recent accumulated information.

Subfamily Brachycoeliinae Looss, 1899

Diagnosis.—With characteristics of the family (Cheng, 1958)[2]; cuticle spinous, more pronounced at anterior end of body; intestinal ceca short, never extending posterior to acetabulum; gonads in middle one-third of body, ovary anterior to testes; vitellaria never extending posterior to level of testes; genital pore between acetabulum and crural fork; excretory vesicle Y-shaped with extremely short cornua.

Type genus.—*Brachycoelium* (Dujardin, 1845); so designated by Looss (1899).

Subfamily Leptophallinae Dayal, 1938

Diagnosis.—With characteristics of family; cuticle completely spinous; intestinal ceca of medium length, reaching through two-thirds of body; ovary anterior to testes; vitellaria limited to exterior one-third of body; genital pore between acetabulum and crural fork; excretory vesicle Y-shaped with extremely short cornua.

Type genus.—*Leptophallus* Lühe, 1909; so designated by Dayal (1938).

Subfamily Mesocoeliinae Dollfus, 1929

Diagnosis.—With characteristics of family; cuticle spinous or aspinous; intestinal ceca of medium length, either limited to anterior

[2] The familial characteristics of Brachycoeliidae given by Cheng (1958: 68) as those of the subfamily Brachycoeliinae which taxon has since been elevated to familial rank.

one-half of body or extending beyond middle of body, never reaching posterior margin of body; testes anterior to ovary; vitellaria lateral to ceca, may intermingle along medial line, never extending to posterior margin of body; excretory vesicle I or Y-shaped.

Type genus.—*Mesocoelium* Odhner, 1911; so designated by Dollfus (1929).

KEY TO THE SUBFAMILIES OF BRACHYCOELIIDAE

1. Ovary anterior to testes.
   A. Intestinal ceca short, never extending posterior to acetabulum........ ....Brachycoeliinae Looss, 1899
   B. Intestinal ceca of medium length, reaching posterior limits of middle one-third of body..Leptophallinae Dayal, 1938
   C. Intestinal ceca long, extending short of posterior end of body.......... ....Glypthelminae Cheng, 1959
2. Ovary posterior to testes; intestinal ceca either limited to anterior one-half of body or extending beyond middle of body, never reaching posterior margin of body............................Mesocoeliinae Dollfus, 1929

THE GENUS CYMATOCARPUS

In 1899 Looss established the genus *Cymatocarpus* to receive *C. undulatus,* a parasite of the intestinal tract of *Thalassochelys corticata* from Egypt. This genus was tentatively assigned to the family Dicrocoeliidae although the reasons for this designation was never given. In 1899 Braun described *Distomum soleare* from *Chelone mydas,* and later, in 1901, transferred this species to the genus *Cymatocarpus.*

Linton (1910) identified specimens of *C. undulatus* from the intestines of the loggerhead turtle, *Caretta caretta,* captured at the Marine Laboratory of the Carnegie Institution, Tortugas, Florida. Neither Braun (1899, 1901) nor Linton (1910) attempted to place *Cymatocarpus* in any definite family. A search through the literature revealed that the three above mentioned references are the only existing ones. A careful search for unassigned trematodes which might be considered members of the Brachycoeliidae revealed a startling similarity between *Cymatocarpus* and *Brachycoelium.* The two species of *Cymatocarpus* both possess short intestinal ceca of the type found in the members of *Brachycoelium;* an ovary which is situated anterior to the testes; an anterior sucker and an acetabulum of subequal size, situated in the anterior half of the body; a genital pore which is situated anterior to the acetabulum; ascending and descending uterine limbs; a Y-shaped excretory vesicle; a seminal receptacle, a Mehlis' gland and a Laurer's canal. These characteristics are all common to the species of *Brachycoelium,* in fact, *C. undulatus* and *C. solearis* could almost be considered members of *Brachycoelium* except for the extremely large cirrus pouch which is characteristic of both species. The length of the cirrus pouch in *Cymatocarpus* ranges from 5 to 7 times the diameter of the acetabulum. This peculiar condition is

considered to be of sufficient significance to warrant the recognition of *Cymatocarpus* as an independent genus assigned to the subfamily Brachycoeliinae.

The abbreviated diagnoses of *Cymatocarpus undulatus* and *C. solearis* are given here, as are the original illustrations, to facilitate the identification of the two species.

Cymatocarpus undulatus Looss, 1899
Figure 1

Diagnosis.—Body elongate oval, 2-5.5 mm long, 1-2 mm wide; cuticle spinous; anterior sucker 0.28 by 0.28-0.3 mm, acetabulum 0.24-0.28 mm; prepharynx obscure, pharynx small, 0.09-0.15 mm in diameter, esophagus slender and extremely long; intestinal ceca short, not extending posterior to level of acetabulum; testes irregularly oval, 0.335-0.337 by 0.58-0.67 mm, situated side by side, posterior to acetabulum; cirrus pouch extremely large, approximately 6 to 7 times the diameter of acetabulum in length, containing seminal vesicle and armed cirrus; number of bursae at base of cirrus (4 small and 2 large) lined with fine spines; ovary, 0.2-0.28 by 0.15-0.18 mm, anterior to left testis, posterior to acetabulum; vitellaria lateral, extending from

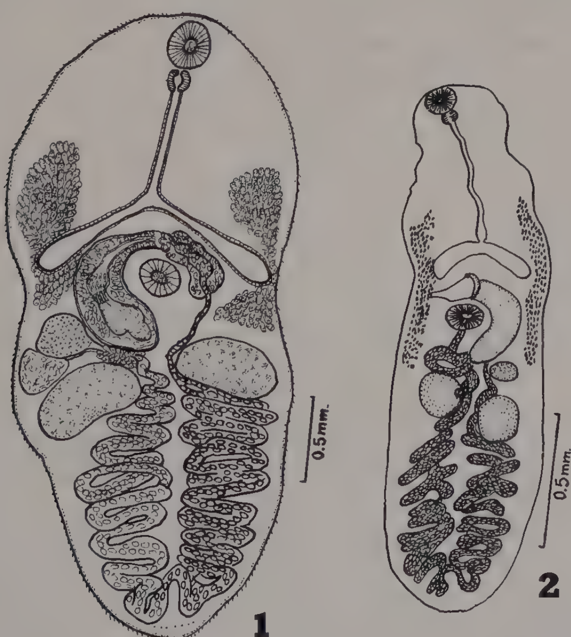

Fig. 1.—*Cymatocarpus undulatus* Looss, 1899. (After Looss, 1899). Dorsal view. 2.—*Cymatocarpus solearis* (Braun, 1899). Dorsal view.

level of midlength of esophagus to beyond cecal tips; ascending and descending limbs of uterus not intercoiled; metraterm with thick glandular wall. Eggs 0.023-0.025 by 0.015 mm.

Type host.—*Thalassochelys corticata.*
Type locality.—Abukir, Egypt.
Type specimen.—Not extant.

Cymatocarpus solearis (Braun, 1899)
Figure 2
Syn. *Distomum soleare* Braun, 1899

Diagnosis.—Body elongate; cuticle aspinous; 2 mm long, 0.6 mm wide; anterior sucker 0.13-0.14 mm in diameter, acetabulum subequal to anterior sucker; prepharynx absent, esophagus long (0.5 mm); intestinal ceca short, not reaching level of acetabulum; testes kidney-shaped, 0.15-0.16 mm in diameter, posterior to acetabulum, slightly oblique, left one slightly anterior to right; ovary 0.07-0.09 mm in diameter, anterior to right testis but posterior to acetabulum; cirrus pouch large, approximately 4 times diameter of acetabulum in length, containing seminal vesicle, unarmed cirrus and prostate glands; no spinous bursae present; vitellaria laterally situated, from level of posterior one-third of length of esophagus to level of anterior margin of left testis; ascending and descending limbs of uterus not intercoiled; metraterm without thick glandular wall. Eggs 0.014 by 0.008 mm.

Type host.—*Chelone mydas.*
Type locality.—New Guinea.
Type specimen.—Not extant.

DISCUSSION

Cymatocarpus undulatus can be distinguished from *C. solearis* by its armed cirrus, spinous bursae at the base of its cirrus, its larger cirrus pouch, its greater body width (1-2 mm wide in *C. undulatus,* 0.6 mm in *C. solearis*), its larger eggs (0.025 by 0.015 mm in *C. undulatus,* 0.014 by 0.008 mm in *C. solearis*), and by its spinous cuticle.

Yamaguti (1958) in his commendable monograph of the digenetic trematodes, also considers the genus *Cymatocarpus,* along with *Brachycoelium,* to be a member of the Brachycoeliinae; however, he does not consider Leptophallinae to be subordinate to the Brachycoeliinae, and since Glypthelminae was not erected until after the publication of his monograph, it was not considered. Yamaguti considers the Leptophallinae a subfamilial group under the Plagiorchiidae, a designation with which the authors cannot agree. Recently Dr. E. H. Cordero (personal communication) stated that the Mesocoeliinae should be considered as an independent family, Mesocoeliidae, however, for reasons which will be presented in a later part

of this series, the authors must consider Mesocoeliinae as a subfamily under the Brachycoeliidae.

No complete life history study is known within the genus *Cymatocarpus*. However, Dollfus (1927) reported the finding of the metacercarial stage of *C. undulatus* encysted in the abdominal muscles of *Pagurus tinctor*. It is not known whether this crab serves as the only or the second intermediate host, and hence until the complete life history is known this information is of little value taxonomically, since it is assumed, from the few life histories known among the members of the Brachycoeliidae, that all of the genera utilize only one intermediate host. It is strongly suspected, however, that *P. tinctor* is the only intermediate host, since in those forms where the life histories are known the metacercaria is found (encysted or unencysted) within the invertebrate host.

KEY TO THE GENERA OF BRACHYCOELIINAE

1. Length of cirrus pouch never greater than twice the diameter of the acetabulum..*Brachycoelium* (Dujardin, 1845)
2. Length of cirrus pouch 4-7 times the diameter of the acetabulum...*Cymatocarpus* Looss, 1899

KEY TO THE SPECIES OF CYMATOCARPUS

1. Cirrus unarmed; no spinous bursae present at base of cirrus...*C. solearis* (Braun, 1899)
2. Cirrus armed; spinous bursae at base of cirrus...*C. undulatus* Looss, 1899

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Calamovilfa longifolia and Its Variety magna

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Chicago Natural History Museum

The grass *Calamovilfa longifolia* was described by Hooker (1840) from a collection made in Saskatchewan. Fifty-one years later, Lamson-Scribner and Merrill (1901) recognized a variety of *C. longifolia* that they named *magna,* distinguished from the species "mainly by its large size." In subsequent years this variety has been accepted by some authorities (e.g., Fassett, 1951; Gleason, 1952; Hitchcock, 1935, 1950; and Shinners, 1943) and ignored, overlooked, or not regarded as distinct by others, presumably equally competent (e.g., Deam, 1940; and Fernald, 1950). Those who recognize the variety maintain that it may be distinguished from the species by several characteristics: the greater size of the plant; the greater size of the panicle; the greater spread of the panicle branches; the color of the spikelets; the presence of a tuft of hairs at the summit of the pedicel; the presence of pubescence on the leaf sheaths; and its geographic distribution.

During the summer of 1958 field studies and mass collections of *C. longifolia* were made over much of its range. The analysis of the mass collections and the results of a study of about 1,200 herbarium specimens[1] are the subject of the present paper.

Acknowledgments.—I extend my thanks to Chicago Natural History Museum, whose sponsorship of my 1958 field work made this study possible; to the curators of the various herbaria who made specimens of *Calamovilfa longifolia* available to me; to Chester E. Hansen, faculty member at York Community High School, Elmhurst, Illinois, and my wife, Mildred W. Thieret, who assisted in the onerous task of making the mass collections; and to Samuel H. Grove, Jr., of Chicago Natural History Museum, who drew Figures 1 and 2.

One hundred and twenty-eight mass collections of *C. longifolia* were made in the following states or provinces (see Fig. 1): Alberta (4), Saskatchewan (2), Montana (4), Wyoming (12), North Dakota (1), South Dakota (22), Nebraska (21), Illinois (18), Wisconsin (9), Indiana (3), Michigan (24), and Ontario (8). Each mass collection was from a presumed clone and consisted of two complete culms and usually 12 to 14 inflorescences chosen to represent variation and frequency of variation of size and shape. A total of 1,588 panicles was collected and carefully pressed to retain, as much as possible in two dimensions, natural appearance. For

[1] From these herbaria (abbreviations those of Lanjouw and Stafleu [1956]): ALTA, CAN, COLO, DAO, F, GH, ILL, ILLS, IND, ISC, KSC, MICH, MIN, MO, MONT, NDA, NEB, NY, RM, SASK, SDC, TRT, UBC, UMO, US, WIS, and WS.

specimens collected in the central and northern plains this was no problem because the inflorescences there are for the most part narrow and rather spike-like. The Great Lakes and western Illinois specimens, however, often have panicles so large and spreading that it was sometimes necessary to divide a panicle into two or three sections and press each in a separate sheet. Representative material from each of the mass collections is deposited in the herbarium of Chicago Natural History Museum.

There can be no doubt that variety *magna* is distinct from the typical form of *C. longifolia,* hereafter referred to as variety *longifolia.* Those who question this should observe the grass in the field in, say, the Badlands of South Dakota or the sand hills of Nebraska and then in Indiana Dunes State Park in Indiana or Ipperwash Provincial Park in Ontario. The Great Lakes plant is, to use the words of Shinners (1943), "utterly dissimilar in its appearance in the field." To distinguish the two varieties in the field and on herbarium specimens (almost all of the herbarium specimens I have examined can be placed at a glance into one variety or the other) is one matter, but to record in print the often difficult-to-define differences is quite another.

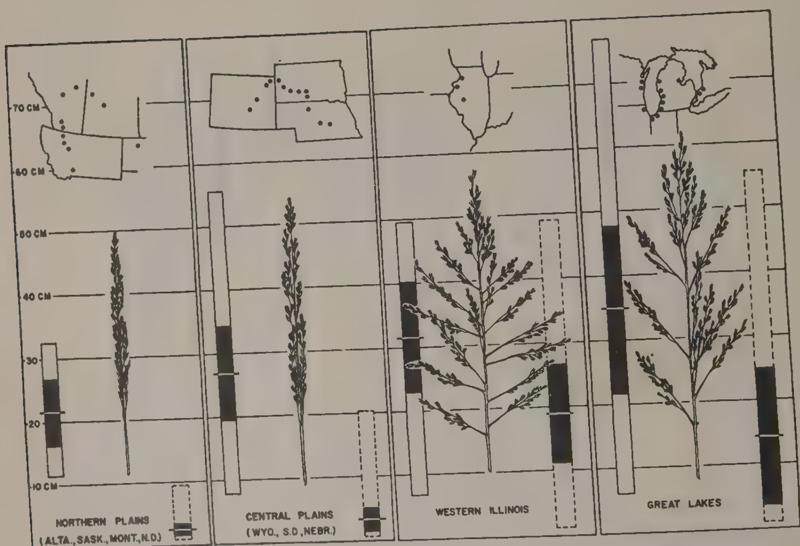

Fig. 1.—Graph summarizing mass collection data on variation of length and width of panicles of *Calamovilfa longifolia.* Solid-line rectangles represent range of length, dotted-line rectangles range of width. Mean figures are represented by cross bars. Shaded areas represent standard deviations from the means. Panicles drawn show "average" specimens. Dots in maps indicate areas where mass collections were made.

Size of the plant.—Culms of var. *magna* average 3 to 4 decimeters taller than those of var. *longifolia.* However, the same maximum height, 23.4 dm, can be reached by culms of each variety. The range of culm height in several presumed clones is as follows:

var. *magna*	var. *longifolia*
11.2 - 16.2 dm	8.6 - 11.2 dm
12.7 - 23.4 dm	9.1 - 11.7 dm
10.7 - 13.2 dm	16.5 - 23.4 dm
6.3 - 12.7 dm	9.9 - 18.3 dm
7.6 - 15.2 dm	6.6 - 10.2 dm
11.2 - 20.8 dm	4.1 - 6.1 dm
19.0 - 21.6 dm	6.1 - 15.2 dm

It is evident from these figures that var. *magna* cannot be distinguished from var. *longifolia* "mainly by its large size," as stated in the original description of *magna.*

Inspection of the data in Table I and of the graph in Figure 1 indicates that, on the average, panicles of var. *magna* are longer by about 9 cm than those of var. *longifolia.* The amount of overlap in panicle length, however, detracts considerably from the usefulness of this character. Panicles are, on the average, considerably wider in *magna* (by about 14 cm) than in *longifolia,* and there is much less overlap in width than in length. A still more useful characteristic to distinguish the varieties is the ratio of panicle length to panicle width (l/w). Panicles of *longifolia* average about 10 times as long as broad, while those of *magna* average only 3 times as long as broad. Panicle branches of *magna* attain greater lengths — up to 33 cm — than those of *longifolia,* which reach as much as 23 cm only rarely. The width of the panicle in either variety depends in part upon the amount of divergence of the branches, a characteristic discussed in the following paragraph.

Spread of the panicle branches.—The amount of divergence of the panicle branches furnishes an excellent characteristic to set apart the varieties. In *longifolia* the panicle branches are usually appressed or strongly ascending (angle of divergence less than 15°). However, panicles of *longifolia* can be found wherein the lowest branches diverge as much as 50°, but even in these panicles the branches in the terminal third of the panicle are appressed or strongly ascending.

TABLE I.—Panicle size (in centimeters) in two varieties of *Calamovilfa*

	magna			*longifolia*		
	Length	width	l/w	Length	width	l/w
mean and standard deviation	33.7± 11.3	16.8± 9.6	3.4± 2.1	24.4± 6.4	3.0± 1.3	10.3± 3.6
maximum	77.5	57.0	16.2	55.5	20.8	36.7
minimum	6.3	0.7	0.9	7.9	0.8	1.6

Panicle branches of *longifolia* are comparatively rigid. In *magna* the often flexuous or lax panicle branches are mostly strongly divergent, commonly exceeding 50° in the lowest third of the panicle, and some branches, especially the basal, may be reflexed.

Color of the spikelets.—The basic color of the spikelets of *longifolia* is a straw yellow that approaches reasonably close to the "cream color" of the Ridgway standard (Ridgway, 1912). It may, however, be slightly lighter or somewhat greenish tinged. A violet-purple, approaching the "dark hyssop violet" of Ridgway, may overlay the basic "cream color," appearing only as a trace on the glumes or becoming more general over the glumes, lemma, and palea, and even spreading to the anthers. When growing side by side, the color extremes — a clone with "cream color" panicles without a trace of anthocyanous pigmentation and a clone with panicles deeply suffused with "dark hyssop violet" — are strikingly distinct and suggest that the color differences are genetically controlled. The amount and intensity of the "dark hyssop violet" appear to be influenced to some extent by exposure to light.

As in *longifolia,* the basic color of the spikelets of *magna* is "cream color," and over this may be laid varying amounts of "dark hyssop violet." However, with or without this "dark hyssop violet" a brownish cast may be laid over the "cream color." When present, as it commonly is in *magna,* this brownish cast is a useful characteristic to distinguish the varieties, giving to panicles of *magna* a different appearance colorwise from those of *longifolia,* which only very rarely have this brownish cast.

Pedicel hairs.—This characteristic is used by Fassett (1950) as follows: var. *longifolia,* "summit of pedicels always glabrous"; var. *magna,* "often with a tuft of hairs at the summit of the pedicel." Unfortunately these distinctions do not hold. Of the 818 panicles of *longifolia* examined by me, 47 percent showed at least a few hairs on the summits of some of the pedicels. Of 770 panicles of *magna,* 58 percent showed pedicel hairs. These hairs occur more frequently in *magna* than in *longifolia* and mostly in greater numbers per pedicel. However, too much overlap in this character renders it of little taxonomic use.

Pubescence of the leaf sheaths.—Each of the 124 culms of *magna* collected by me had at least some pubescence on the leaf sheaths, especially the lower. In contrast, only 12 percent of 132 culms of *longifolia* had pubescent leaf sheaths. Most plants of both varieties have at least some pubescence on the collar or collar margins whether or not the sheath is pubescent. Sheath pubescence in *longifolia* is usually slight and mostly restricted to or heaviest at or near the margins, although plants occur with copious pubescence over the entire sheath. *Magna* sheaths are usually heavily pubescent, but may be

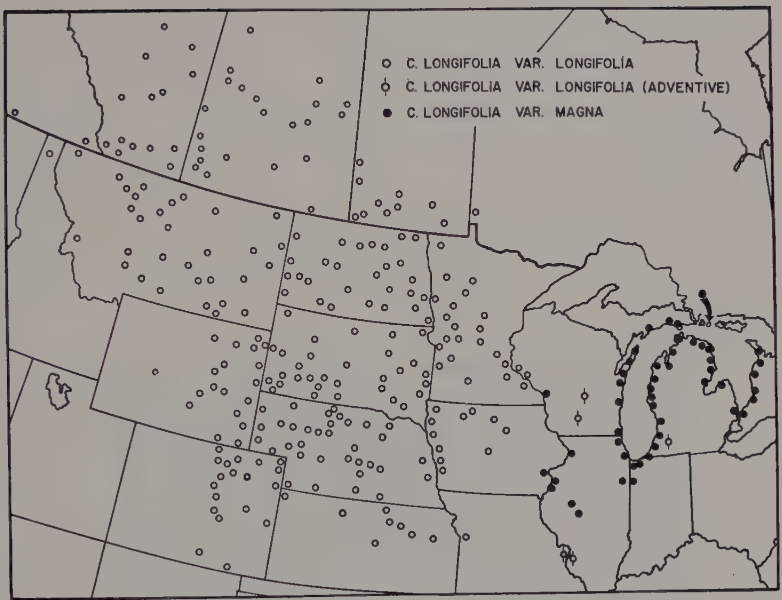

Fig. 2.—Distribution of *Calamovilfa longifolia.*

lightly so or rarely even glabrous (as in R. W. Pohl No. 1088, Kenosha Co., Wisconsin [MICH, MIN, WIS]).

Geographic distribution.—Var. *longifolia* is a characteristic grass of many drier prairies on the interior plains of the United States and southern Canada (Fig. 2). It is usually found in sand or sandy soil but occasionally in clay soil or loess. Its growth seems to be especially vigorous in disturbed soil. Its western limit coincides reasonably well with the western limit of the Great Plains province, although outlying stations occur in dry grasslands in the Cordilleran region. To the north the grass extends throughout the grassland and parkland of Canada's prairie provinces and enters slightly into the southern portion of the boreal forest where it occurs on sand dunes, sandy pinelands, and sandy prairies. It reaches a southern limit in southeast Colorado and an eastern limit in southwest Wisconsin. It has been found as an adventive in south central Wisconsin, the St. Louis area, and southwest Michigan.

Var. *magna* is a characteristic grass of dunes — especially those that are active and semi-established — and sandy shores fringing Lakes Michigan and Huron (Fig. 2). It is an excellent sand binder. Inland stations occur on sand or sandy soil in northwest Indiana, northeast, west and central Illinois, southeast Iowa, and southwest Wisconsin.

Noteworthy collections of *C. longifolia* are cited below.

C. longifolia var. *longifolia*

Northernmost collection (lat. 54° 20′ 30″). Waterhen River crossing 25 miles north of Meadow Lake, Saskatchewan, A. J. Breitung 8263 (DAO).

Southernmost collection (lat. 37° 10′ 10″). Sandy soil, side of Mesa de Maya, 3 miles south of Tobe, Las Animas Co., Colorado, C. M. Rogers 5031 (COLO).

New to British Columbia. Kettle Valley, British Columbia, H. K. DeBeck s.n. (UBC); Tobacco Plains, north of Flagstone, British Columbia, J. W. Eastham s.n. (DAO, US).

New to Ontario. Dry, gravelly soil, Ingolf [southwest] Ontario, W. N. Denike 1320 (DAO).

Fig. 3.—Panicles of var. *longifolia* (left) and var. *magna* (right) to show difference in density of inflorescence. The panicle of *longifolia* is an atypically open one.

C. longifolia var. *magna*

New to Iowa. Sand, Moose Lodge area, Muscatine Island, Louisa Co., Iowa, B. Shimek s.n. (ISC).

Density of the inflorescence.—An excellent criterion to distinguish the varieties is the density of the inflorescence. In *longifolia* the spikelets are relatively closely imbricated so that transverse lines laid across a branch usually cross 2 or 3 (sometimes 4) spikelets. In *magna,* on the other hand, usually only 1 or 2 spikelets are crossed because the spikelets are less closely imbricated. The relative density of the inflorescences of *longifolia* and *magna,* difficult to express verbally, can best be appreciated by observing the panicles themselves (see Fig. 3).

A description of *Calamovilfa longifolia* and a key to its varieties follow.

Calamovilfa longifolia (Hook.) Scribn. A coarse perennial grass, culms bunched or solitary, to 23.4 dm high, with elongate, scaly, pointed rhizomes and tough, wiry roots. *Leaves* rolled in the bud; sheaths to 15 cm in length, open, with mostly overlapping hyaline margins, glabrous to densely villous; blades to 64 cm long, 12 mm wide at the base, firm, flat to involute, tapering to a long thin tip; collar distinct, broad, continuous, yellowish, usually pubescent on the margins; ligule a dense fringe of hairs to 3 mm long. *Panicles* up to 77.5 cm in length, long-exserted to included at the base, contracted and narrow to open and broad, the branches tightly appressed to widely spreading, the lower sometimes reflexed. *Spikelets* awnless, to 8.5 mm long (usually 5-7 mm), basically straw color but often overlaid with varying amounts of violet-purple and/or brown; glumes acute, one-nerved, glabrous, subequal to unequal, the second the longer; lemma and palea subequal, glabrous, slightly shorter than, equal to, or longer than the second glume; lemma one-nerved, palea furrowed between its 2 nerves; callus densely bearded with silky hairs ½ to ⅞ the length of the floret; anthers 3 to 5 mm long.

KEY TO VARIETIES

Panicles mostly 1.3-5.5 times as long as wide, mostly 7.3 - 26.4 cm wide, up to 77.5 cm long. *Panicle branches* up to 33 cm long, typically widely spreading, diverging often more than 50° in the lower third of the inflorescence, sometimes reflexed. *Spikelets* commonly with a brownish cast, relatively loosely imbricated. *Leaf sheaths* usually pubescent, often densely so, rarely glabrous. Plant of the shores of Lakes Michigan and Huron, also outlying stations in southeast Iowa, in northeast, west, and central Illinois, in southwest Wisconsin, and in northwest Indiana.......................................var. *magna* Scribn. & Merr.

Panicles mostly 6.7 - 13.9 times as long as wide, mostly 1.7 - 4.3 cm wide, up to 55.5 cm long. *Panicle branches* up to 23 cm long, usually much shorter, typically appressed or strongly ascending, at least in the upper third of the inflorescence. *Spikelets* only rarely with brownish cast, relatively closely imbricated. *Leaf sheaths* mostly glabrous, infrequently lightly pubescent, rarely densely so. Plant ranging from extreme south-

west Ontario north and west to central Saskatchewan and Alberta, southeast British Columbia, south and west to southwest Wisconsin, northwest Missouri, southeast Colorado, east Wyoming, and northern Idaho, rarely adventive further east..var. *longifolia*

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Correlation of a Population of Roof Rats in Venezuela with Seasonal Changes in Habitat

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The purpose of this study is to obtain a better understanding of the forces acting on the rodent population in Venezuela. The site of the study is Zorro Island in Lake Valencia (Tacarigua). This locality was chosen because it is inhabited by a colony of *Rattus rattus rattus*, the size is adequate, there is little possibility of migrations, and meteorological data are readily available. The study began April, 1956; it still continues but the data presented cover only the period from that date to January 1958.

Lake Valencia, in the North Central part of Venezuela is 33 km long, 18 km wide and has an average depth of 30 m. The level of the lake varies according to the season, but the average altitude of its surface is about 400 meters above sea level. There are 20 islands or protruding rocks.

Zorro Island is the fifth largest island and is located in the southeastern part of the lake (10° 09′N 67°39′W) (Fig. 1). Its maximum dimensions are 450 m by 225 m, and its area is 6.5 hectares. The maximum height above lake level is 43 m. The shortest distance to other land areas, the Iguana Peninsula, is 750 m. Actually the distances are rough averages for the duration of the study, as the shore line changes due to the seasonal fluctuations of about a meter in the level of the lake's surface. Also, the general trend is for this level to decrease, having lost about 20 m since 1727.

The island's origin has been traced to the Tertiary geological era. It was formed by projected masses of rocks and eruptive adjustments. The surface is composed of a steep central hill surrounded on the east, south, and west sides by a crescent-shaped, terraced, gradually-sloping area that has emerged due to the decrease of the level of the lake. Based on this formation the island can be divided into four general areas: (a) shore, narrow strip of rocks with occasional coarse sand beaches; (b) emerged zone, largest component of the study sites; the basic soil is an accumulation of loam, humus, pebbles and small rocks that increase in size towards the central hill. The average slopes are: east side 30 percent, south 16 percent, west 23 percent. There is an unusual narrow vein of sandy loam traversing the southern part; (c) central hill, steep, 74 percent slope and formed by clusters of large rocks based over a rock bed; (d) hilltop, rather flat and with a surface similar to that of the emerged zone suggesting that the entire island was covered by water at some ancient period.

Natural drainage of the island is excellent, and no surface water is found. The lake water is quite brackish with a pH value of 8.8

and a salinity of 1.1 ppm which is increasing at a yearly rate of 3.4 parts per million. Rainfall and temperature date for the years of trapping are given in Table I. The rain usually falls in intense periods of short duration separated by fair weather with clear sky. During the peak of the rainy season cloudy days with no direct sunlight may occur. The direction of the wind is quite varied over the lake, but predominantly from the east. Light breezes are normal during the early night and through the morning, changing to gales in the afternoon that produce short white-capped waves one meter or more in height. The intensity of the east wind appears to be uniform throughout the year. At the beginning of the rainy season this wind carries debris from the eastern mainland shore to the eastern shore of the island. The waste consists of tree branches, decomposed local crops,

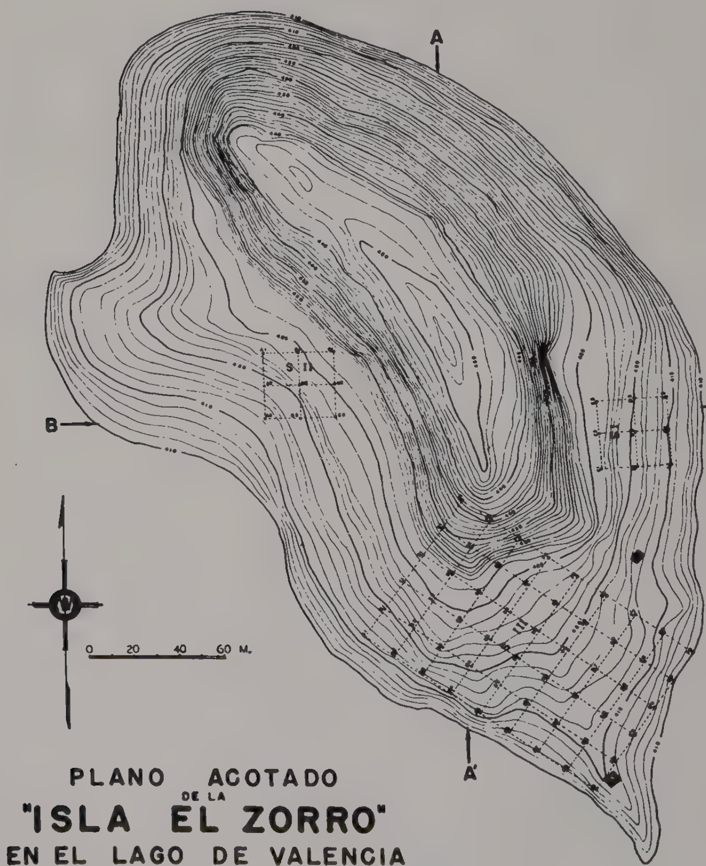


Fig. 1.—Contour map of Zorro Island showing location of grids.

and empty containers and could be the source of some of the animals and plants now living on the island.

VEGETATION

The vegetation of the island is a tropical, deciduous, seasonal forest similar to that of the near mainland. The submerged plants in the lake are represented by the genera *Chara, Nostoc, Potamogeton, Najas* and *Vallisneria* which form colonies close to the shore varying in density according to depth. The emergent vegetation is represented by one species of each genus, *Panicum, Acnida* and *Typha*. Their existence is governed by the fluctuations of the water level, the waves, and the soil. The floating vegetation consists of three genera, each represented by one species, *Pistia, Eichornia*, and *Hydromystria*. Their presence is determined by the winds and currents.

The *Paspalum-Poponax* Zone is a narrow strip of land along the island's perimeter, characterized by the dominant grass (*Paspalum*) in the lower level with occasional intrusion of emergent *Panicum*.

TABLE I.—Rainfall and temperature data for the months when trapping

Year	Month	Total Rainfall mm.	Mean Temp. °C	Mean Percent Humidity
1956	January	18.5	22.8	78
	February	13.5	23.8	74
	March	11.1	24.2	71
	April*	5.9	25.4	70
	May	81.1	25.3	76
	June	87.2	24.7	78
	July	71.1	23.9	81
	August	269.9	23.6	85
	September	104.2	23.8	83
	October	163.4	23.9	83
	November	61.2	23.7	81
	December	67.8	22.5	81
1957	January	6.5	21.8	76
	February	0.2	23.2	71
	March	0.0	24.4	67
	April**	16.3	25.5	69
	May	70.1	25.6	77
	June	88.6	24.6	81
	July	113.9	24.5	81
	August	198.3	24.3	81
	September	112.8	24.6	81
	October	77.6	24.1	81
	November	49.3	24.1	80
	December	1.2	24.4	73
1958	January	0.0	24.3	70

* rain for first time the last week of April
** rain for the first time the night of the 12th.

In the canopy the tree *Poponax* is abundant. Many vines, bromeliads, and other arboreal forms are present on these trees.

The *Capparis* Zone ranges up to the base of the central hill and is characterized by the great abundance of three species of *Capparis* forming an intermediate canopy. Also present are two species of cacti and an intricate group of vines (*Cissus, Serjania, Elaterium*) covers the trees and sometimes rocks and fallen trunks. Among the eleven species of smaller plants forming the underbrush by far the most numerous are *Petiveria* and young *Capparis*.

The *Bursera* Zone occurs around the base and slope of the central hill where the tall *Bursera* forms a dense canopy. Other large trees are found, including some unidentified legumes. The underbrush is similar to that in the *Capparis* zone, but is heavier and includes impenetrable barriers formed by great clusters of *Petiveria* and the thorny *Acanthaceae*.

The *Tabebuia* Zone at the crown of the hill consists of a dense colony of *Tabebuia,* up to 8.0 m in height, dominating over other vegetation formed mostly by *Cereus, Peireskia, Capparis, Bursera, Coccoloba,* and cacti. The underbrush is composed of a varied group of grasses; one of them, a very small type of bamboo, forms dense colonies.

The species occurring on the three sides of the hill show no striking differences in the small sample available along the transect. However, some minor differences occur between the vegetation of the hill and the surrounding zone (Table II). Nevertheless the area is considered sufficiently homogeneous in vegetation to permit its treatment as a unit for some aspects of the population description.

FAUNA

The fauna, like the flora, is a selection derived from the mainland species, and its origin is partly due to wind and water transportation as mentioned in the discussion of the meteorological data. It is beyond the scope of this study to give a complete list of the varied fauna on the island and only the most prominent will be mentioned. There are no Amphibia on the island. The amphibious reptiles are plentifully represented by a small alligator and some turtles, the latter introduced from the llanos. Also found are a great number of small

TABLE II.—Summary of some aspects of vegetation

	Part of Island				
	East	South	West	Hillside	Hilltop
Trees: Number per 10 m ²	7.3	6.8	7.1	2.0	4.5
Average height (m)	5.0	5.6	5.8	8.0	7.0
*Canopy cover (percent)	85.0	75.0	95.0	60.0	70.0
Underbrush: Cover (percent)	36.0	41.0	63.0	95.0	80.0
Height (m)	0.3	0.8	0.9	1.5	0.5

* August at noon

lizards, mostly geckos and iguanas, and an unidentified species of nonpoisonous snake. The birds include water turkeys and kingfishers along the shore, and woodpeckers, doves, flycatchers, egrets, troupials, and oropendolas on the island. Among the many seasonal visitors are hawks, hummingbirds, vultures, blue-winged teal, and parrots.

At the beginning of the study opossums (*Didelphis marsupialis*) created a problem by springing, displacing, and occasionally damaging the traps. The problem was solved by building special traps and removing the captured opossums to other islands. A total of 7 individuals was caught during the first two months and after that no more were noticed. Other mammals present are a few colonies of bats and rodents, primarily of the genus *Rattus;* on rare occasions members of *Cricetinae* (species unidentified) and *Mus musculus* have been caught, released, and never observed again. The presence of *Cricetinae* is assumed to be due to sporadic immigration by natural means, while that of *Mus* is due to transportation by boat from the north shore of the lake.

SEASONAL CHANGES

The seasonal changes of the habitat on Zorro Island are marked. From the meteorological data (Table I) it can be observed that the average monthly rainfall is variable, with a high and stable humidity as is expected in a lake habitat. Although the average monthly temperatures present extremes of 3.8° C this range is insignificant when compared to the occasional 7.0° C daily variations. The length of daylight does not change much during the year on account of the proximity to the equator.

Detailed measurements of changes of vegetation and of food were considered too formidable a task for this study and therefore the general changes will be described from observations at each trapping period. The dry season starts in December and lasts till May (Table I). With a few exceptions this periodicity in occurrence is uniform throughout the years but the amount of rain in the rainy season is variable. In January the underbrush has disappeared, only its seeds remain. The trees, with such exceptions as *Ficus, Poponax, Hura* and *Capparis,* have shed all their leaves. Fruits are found in small quantity only on some *Bursera* and the ground is covered by a thick layer of dry leaves. The density of sunlight falling on the terrain has increased greatly. Also, as is common in this type of forest, during this month the trees begin to flower. Animal activity, with the exception of some reptiles and insects, starts to decrease. During February, the iguanas concentrate on the top of the central hill and deposit their eggs in shallow depressions which they excavate in the soft soil. In the following months the dryness increases, most trees are covered with flowers, and thus the island attracts numerous insects and hummingbirds searching for nectar. Below on the ground animal life is scarce and only the shore dwellers maintain their normal activities.

During March or April the first rains fall. Slowly, at first, the trees begin to produce new leaves and the flowers are replaced by fruits. This is also the time when young iguanas make their appearance and soon can be seen in great numbers. The increasing humidity of the ground accelerates the rotting process of the organic matter covering the soil and the land arthropods start to appear. By June, new underbrush is noticeable, and in July many birds can be seen eating fruits and insects and nesting on the island. The parrots are especially attracted by the great quantities of nest-building material offered by the abundant termite "hills." In August and September, the peak of the rainy season, the island is dark, humid, and covered by thick vegetation. The underbrush and vines form intricately harsh, sometimes poisonous and thorny, barriers that interfere with walking. To this can be added the presence of a considerable number of poisonous arachnids and other pests such as ticks and ants. Usually after September the amount of rain decreases steadily. The first notable change is the reduction in the number of trees with fruits. By November these have all but disappeared and the leaves begin to fall. At this time the underbrush is drying fast and the arthropods are becoming scarce. December marks the end of the rainy season; most trees are leafless and the only fruits, in small quantity and dry, are found on *Bursera*. The arthropods and underbrush are almost nonexistent and seeds from small plants can be seen on the ground. Again, animal activity decreases and the changes in conditions lead to a repetition of the yearly cycle already described. As far as known Zorro Island has not been inhabited by man and so it remains rather unaffected by human use.

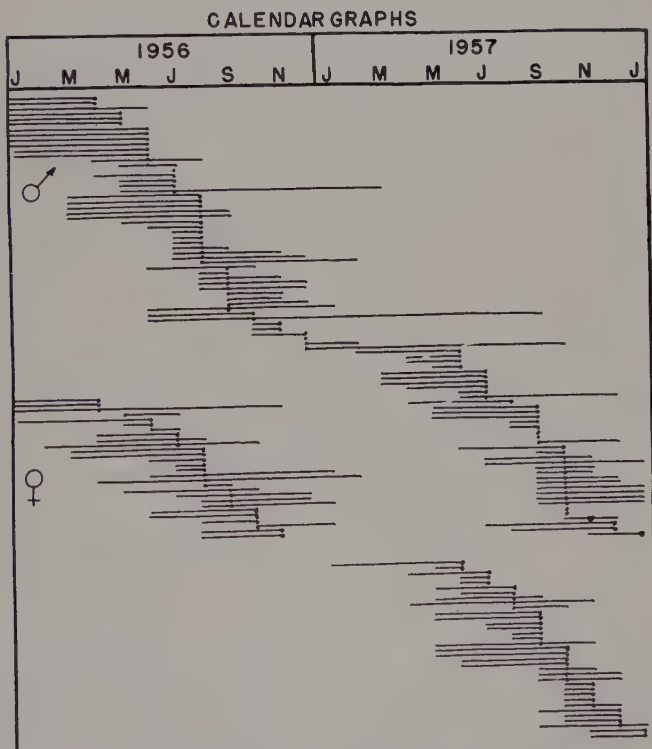
METHODS

The data for the description of the area were obtained from observations and available sources. A complete topographical map of Zorro Island was made for the study using standard survey methods, based on 0.5 m contour curves. The soil description is based on surface observations. The meteorological data were supplied for Zorro Island by the meteorological service of the Venezuelan Air Force which maintains a number of stations around the lake. The description of flora, fauna, and their seasonal changes are based on personal observations. The quantitative estimates of leaves, flowers, fruits, and underbrush and seeds are based on the observation of 10 sample areas, each 15 x 15 m and distributed over the island.

The study of the *Rattus* population is based on the application of the methods, concepts, and assumptions described by Davis (1956). The descriptions that follow only apply to such cases where the method used or some specific detail differs from the text of Davis's manual. In general the method consisted of placing traps in a grid pattern. These traps were set and inspected each morning for 4 or 5 days each month. The captured rats are weighed, marked, inspected for sexual development, and released. The population estimate is

based on the proportion of recaptured individuals in each monthly sample.

The traps were placed on the southern part of the island in a normal grid of 6 x 9 lines 15 m apart. In the east and west they were in parallel lines at the same distance apart but only covering the available space. On the hill and north side a few traps were scattered to detect any presence of rats. A total of 137 traps was normally in use. The traps were rectangular in shape and approximately 35 x 11 x 11 cm in size. Peanut butter, corn, and other cereals



MALES:																								
ADULTS	3	6	12	12	15	14	12	13	10	11	12	9	4	5	3	3	6	10	10	6	10	7	14	12
IMMATURE	3	6	0	5	2	5	5	6	5	3	3	0	2	0	1	3	4	4	3	3	3	D	1	1
BIRTHS	6	0	5	2	5	5	7	5	3	3	0	3	0	1	3	4	4	3	3	3	12	3	1	0
TOTAL	12	12	17	19	22	24	24	24	18	17	15	12	6	6	7	10	14	17	16	14	25	20	16	13
FEMALES																								
ADULTS	0	3	4	5	5	8	9	10	8	13	8	6	4	6	1	1	1	3	9	11	11	7	7	8
IMMATURE	3	1	1	2	3	3	5	4	6	0	1	0	0	1	0	0	2	8	5	2	3	5	7	2
BIRTHS	1	1	2	3	3	5	3	6	0	1	0	0	1	0	0	2	8	5	2	3	5	7	2	0
TOTAL	4	5	7	10	11	16	17	20	14	14	9	6	5	7	1	3	11	16	16	16	19	19	16	10

Fig. 2.—Calendar graph for rats (see text for explanation).

were used as bait during the first month, but the infestation of the traps by spiders, ants, and roaches made it necessary to search for another bait. A very suitable one was found in a local brand of rabbit food. This kept to a minimum the arthropods found inside the traps and was stable during the rainy season. The average number of traps accidentally sprung was about 3 percent. All traps were arranged to capture animals of 20 grams or more but on occasions two individuals of lighter weight have been caught by the same trap.

The populations were estimated in two ways. The first is based on the recapture method. However, although the results fluctuate monthly, the difference between those fluctuations are not significant due to the small size of the sample under study. Because of this a second method was also used. This "calendar graph" method is illustrated in Figure 2. When a rat is captured it is plotted as a dot under the corresponding month. Its weight and sexual development (see later) establishes approximately its month of birth. A line is drawn back to that month. Subsequent recaptures of that individual allow its line to be prolonged forward. To find the number of rats alive each month the lines passing through that month are added. By the distance of any point to the assumed month of birth the state of development of the animal can be estimated and the data separated by sex, age, and births.

This method presents some problems. It gives only the number of individuals known to be alive. It cannot be used for short periods because as the length of study increases, the chances of a recapture for a rat increases, thereby increasing the amount of data. Some difficulties are present when projecting the life of the rat back to the assumed month of birth. These difficulties do not apply to very young individuals but with the placements of the adults, the assumptions have to be made that all rats follow the same development pattern and that this is not affected by seasonal changes or pregnancies.

In order to estimate the population by the calendar graph method the growth needs to be known. Hence, the available data are discussed in the methods section rather than in the results section. The original data are weights of 31 males observed 94 times for periods up to 11 months and of 23 females observed 59 times up to periods of 6 months. Growth is quite uniform for all rats during the first two months. No difference is demonstrated between the growth of males and females. The rates of growth are affected by the dry season according to observations of 19 males followed through that season. In 12 males a loss up to 20 percent in weight was noted at this time, which is regained as soon as the rainy season arrives. The females are affected in the same manner but gain or loss of weight also depends on the relation of the time of observation to pregnancy and parturition.

The sample used for the given growth rates is selected to avoid the influence of the above mentioned factors. The approximated

growth rates for both sexes used in calculating the calendar graph were: 38 grams per month during first month, 27 grams per month for next 2 months, and 15 grams per month from 3 to 6 months.

For interpretation of population estimates and movements some information on susceptibility to capture is important. From Table III it is clear that the frequency of recapture is indistinguishable for the two sexes. Naturally no information is available for the proportion never captured.

RESULTS

Movement of Individuals.—At the beginning of the study only the traps at the southern side caught rodents but by the end of the year the focus of the population had drifted towards the north of the island. To demonstrate this movement quantitatively the percentages of individuals trapped were grouped in consecutive periods of 5 months each starting from April 1956 and ending in November 1957 (Table IV). The distance at which they were caught is given in relation to the hut at the southern tip of the island.

As can be seen the highest group percentage of individuals trapped moves progressively away from the south. These results are difficult to test statistically. However, several biological explanations would agree with the observations. It could be that the population had its origin at the southern shores and is spreading over the island. A few observations support this possibility. a) The *Cricetinae* occasionally trapped, and never seen again, were always found at the south of the island. If the assumption that they are new immigrants is correct, then whatever mode of transportation carried them there could also have carried the *Rattus* to the same place. b) Environmental conditions at the east and west sides are as good as, or better than, those at the south but no rats were found there during the early part of the

TABLE III.—Number of captures of males and of females

Times captured	Males Number	Males Percent	Males Cumulative	Females Number	Females Percent	Females Cumulative
1	46	51.6	51.6	30	46.9	46.9
2	16	18.0	69.6	19	29.7	76.6
3	13	14.7	84.3	9	14.1	90.7
4	4	4.5	88.8	2	3.1	93.8
5	4	4.5	93.3	0	0	93.8
6	4	4.5	97.8	0	0	93.8
7	1	1.1	98.9	2	3.1	96.9
8	0	0	98.9	2	3.1	100.0
9	0	0	98.9			
10	1	1.1	100.0			
Total	89			64		
Observations per rat	2.14			2.08		

study. No rat has been caught in the extreme northern part. The center hill appears to be a natural barrier for the rats. None has been trapped at the summit nor have any of those marked in the east or west been captured at the opposite side. Due to conditions emigration seems unlikely.

The movement of individuals was analyzed from the recaptures. The displacement distances increase numerically as the time interval between observations increases but the differences were not statistically significant. Most males were recaptured at the same trap, but some travelled up to 80 meters. Most females were recap-

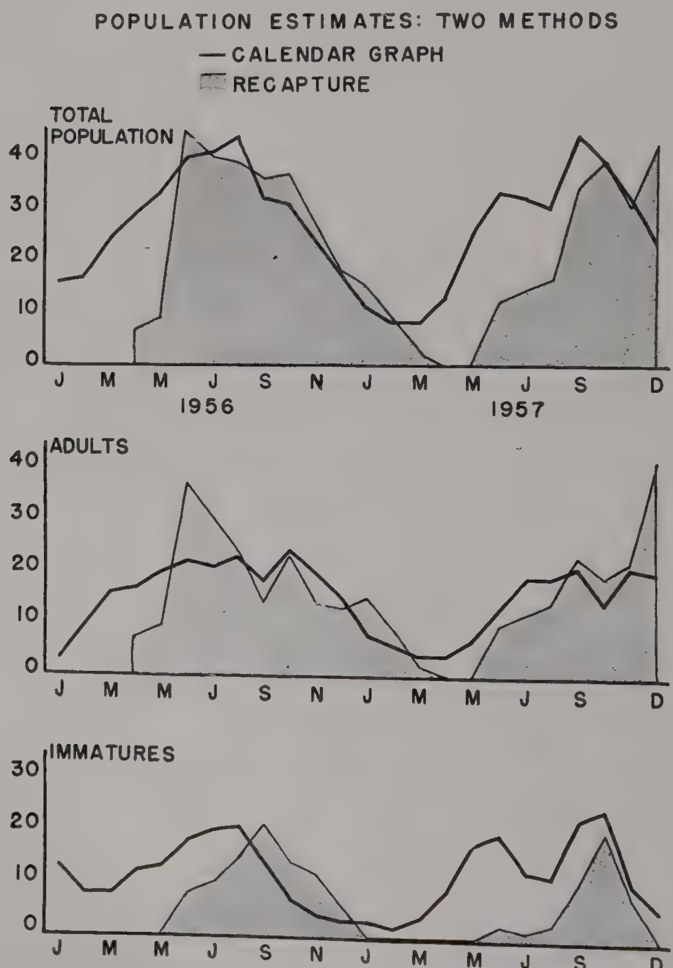


Fig. 3—Population estimates by recapture and by calendar graph methods.

TABLE IV.—Percentage of individuals trapped at distances at southern tip of island

Periods of Observation		Number of rats	Percentage by Distance in Meters 0-15	50-100	100-150	150+
I	April-August	59	29	20	24	27
II	September-January	75	27	31	21	21
III	February-June	14	15	21	43	21
IV	July-November	77	13	7	27	53

tured from 15 to 20 meters away from the original trap, but not much farther. This suggested sexual difference in movement might be induced by the care that the females must give to their young in the nests. The meager data collected for the immatures only hints that their movement is limited. So few observations were recorded during the dry season that no seasonal comparison was possible.

Population Changes.—The two methods used for the population

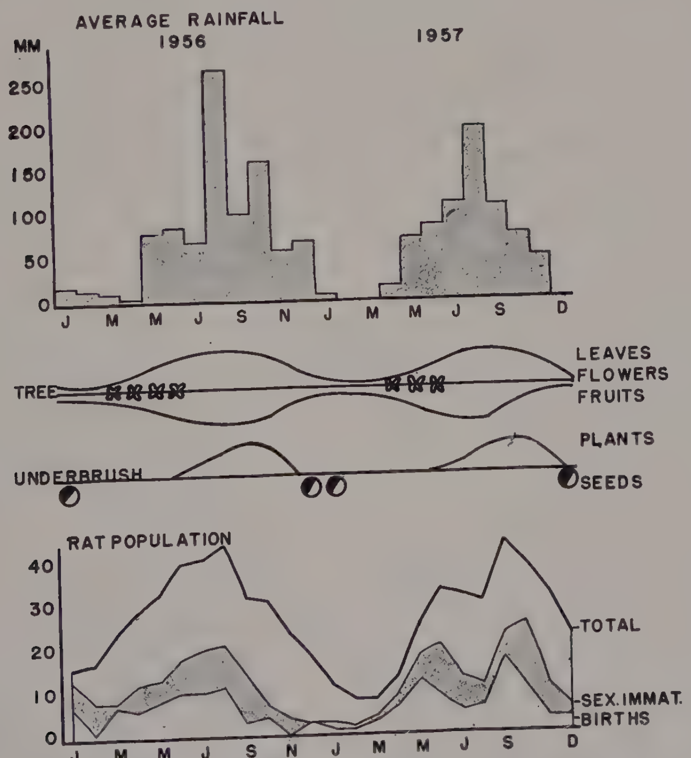


Fig. 4.—Comparison of rainfall and vegetation with rat population.

estimate give similar results (Table V). Figure 3 compares the seasonal variations observed in both the sexually immature and total populations as shown by the two methods. In general the recapture method reports the fluctuations at a later time than does the calendar graph method. This could have resulted from the following: (a) The individual rate of growth is greater than assumed, or (b) since the recapture method deals only with trappable individuals which are above certain weight, while the other method includes them from the moment of birth, a gap is created between the results. This gap is the time required from birth for a rat to become trappable. From the observed individual growth and the fact that not all rats are caught immediately upon reaching the required weight to spring a trap, it is assumed that the lag of the recapture method occurs mostly on account of the second reason given.

The changes in the population curve (Fig. 4) appear to be dependent on the seasonal quantity of animal and vegetable food available to the rats. The curves representing the population for the year 1956 and 1957 are not markedly different. However, in 1956 there is only one peak in the curve while two are present in 1957 for adults and for immatures. Although this difference cannot be demonstrated statistically, it might be the result of two waves of

TABLE V.—Population estimates by two methods (1956-57)

Month (1956-1957)	Total rats caught	Recapture Estimate	Two standard errors	Calendar Graph Estimate Adults	Immatures	Born	Total
Jan.	—	—	—	3	6	7	16
Feb.	—	—	—	9	7	1	17
March	—	—	—	16	1	7	24
April	6	6.7	5.3	17	7	5	29
May	5	9.0	15.0	20	5	8	33
June	13	45.0	85.0	22	8	10	40
July	13	40.0	75.0	21	10	10	41
Aug.	27	39.0	24.0	23	10	11	44
Sept.	20	36.0	29.0	18	11	3	32
Oct.	18	36.7	36.3	24	3	4	31
Nov.	15	25.6	22.4	20	4	0	24
Dec.	15	18.3	9.7	15	0	3	18
Jan.	8	15.0	25.0	8	2	1	11
Feb.	5	9.0	15.0	6	1	1	8
March	2	2.0	3.0	4	1	3	8
April	0	0.0	—	4	3	6	13
May	0	0.0	—	7	6	12	25
June	6	12.0	19.6	13	12	8	33
July	9	14.0	19.8	19	8	5	32
Aug	7	No recaptures		19	5	6	30
Sept.	19	33.8	29.0	21	6	17	44
Oct.	25	39.0	26.0	14	15	10	39
Nov.	18	30.0	24.6	21	8	3	32
Dec.	18	42.0	48.4	20	3	0	23

reproduction, the first from the survivors of the dry season and the second from their progeny.

It is apparent that the initial population was greater in 1956 than in 1957, and hence the peak 1956 population should have been greater than that of 1957. However, the peak population was essentially the same for the two years. Examination of the data suggests that a consideration of the area may provide the explanation. If it is true that the colony is recent and still spreading from its origin at the southern part of the island, then the area occupied by the rats was much greater in 1957 than in 1956. In Table VI it can be seen that in 1956 the grid at the south reached a population nearly twice as large as that of 1957. The population pressure thus created presumably induced more individuals to move north, but then the dry season arrived and stopped the population increment that should have resulted from the presence of rats in other suitable parts of the island.

In 1957 the rats were more evenly distributed over the island, but there are so few individuals left at the beginning of the rainy season that peak local density at the south grid was small.

Distribution.—Observations based on the total number of individuals captured by each trap show that the distribution is correlated with the characteristics of soil and vegetation. The highest population occurs in areas with heavy upper canopy and in the presence of *Peireskia, Cereus, Sapindus,* and other fruit trees where the terrain is relatively clear and rocky. The absence of captures in the center of the population in the south of the island is notable. In this place a very sandy zone is used occasionally for egg-laying by the iguanas. Except in this sandy zone the island's surface offers more than adequate shelter for a population greater than the observed.

Probabilities of Reappearance and Survival.—The recapture method does not give the probability of survival directly because it is not possible to conclude that a rat that is not captured is dead. Although there is a method to calculate probability of survival from recapture data, the small numbers in this study would result in such a large variance that no differences could be demonstrated. However, some biological information can be extracted from the reappearance

TABLE VI.—The maximum population based on two estimate methods

	1956 June-August	1957 September-December
Recapture method:		
Total for island	41.4	38.2
South grid only	29.5	15.8
Percent in south grid	71.3	41.3
Calendar graph (adults only)		
Total adults for island	19.5	20.7
South grid only	12.3	7.7
Percent in south grid	63.1	37.2

of rats in traps. The 29 males and the 21 females (Table VII) that were recaptured at least once were tallied irrespective of season or age according to the number of months between the first and the last capture. For example 42 percent of the males were not captured after the first recapture and 65 percent after the second. In the other part of Table VII the probability of survival from the calculated birth is recorded. Each rat when captured was aged by its weight and then assigned to a month of birth. In this manner the age at last capture was obtained for 82 males and 61 females. The survivals are a minimum because the rats lived for an unknown time after last capture. As expected the probability of reappearance is less than the minimum probability of surviving (Table VII). Because both probabilities are affected by seasonal changes it is superfluous to express them as yearly rates.

The chances of surviving for rats born in the dry season have been compared with survival of those born in the wet season (Table VIII). Rats born in the dry season should survive better (if they reach trappable age), because in about 4 months they would live in the presumably favorable conditions of the wet season. In contrast rats born in the wet season would encounter unfavorable conditions in a few months. Since the difference between probabilities at 3-5 months is statistically significant it can be concluded that the dry season influences the life expectancy of the rats.

Breeding Conditions.—The data available from the trapping (Table IX) were tabulated into four arbitrary seasons that include the following months: (a) Dry: April of 1956, January, February, March and April of 1957. (b) Before rainy: May and June of

TABLE VII.—Reappearance and survival of rats

Months since first capture	Probability of reappearance in traps: 29 males	21 females	Months known to be alive	Probability of survival from calculated birth: 82 males	61 females
1	1.00	1.00	1	1.00	1.00
2	0.58	0.68	2	0.85	0.77
3	0.35	0.43	3	0.68	0.59
4	0.18	0.19	4	0.56	0.41
5	0.12	0.14	5	0.37	0.28
6	0.09	0.09	6	0.05	0.13
7	0.09	0.05	7	0.04	0.09
8	0.09	—	8	0.04	0.07
9	0.06	—	9	0.04	0.05
10	0.06	—	10	0.01	0.03
11	0.03	—	11	0.01	
			12	0.01	
			13	0.01	
			14	0.01	
			15	0.01	

TABLE VIII.—Seasonal differences in minimum probability alive

Months known to be alive	Season of birth: Dry January-June 69 rats	Season of birth: Wet July-December 81 rats
0	1.00	1.00
1	1.00	0.93
2	0.90	0.72
3	0.77	0.47
4	0.68	0.33
5	0.39	0.19
6	0.16	0.06
7	0.10	
8	0.06	
9	0.04	
10	0.04	
11	0.01	

1956, May, June and July of 1957. (c) Rainy: July, August and September of 1956, August, September and October of 1957. (d) After rainy: October, November and December of 1956, November and December of 1957, January of 1958. The months were grouped according to the similarity in their environmental and population characteristics.

The males caught during the dry season were all sexually mature (Table IX). The estimate of the weight at which 50 percent are mature has a low value of less than 50 grams (Fig. 5). In the next season, although some immature individuals are present, the maturity midpoint increases. Presumably a better food supply allows the rats to gain weight and thus weigh more when attaining sexual

TABLE IX.—Breeding conditions of rats by seasons

	Dry	Before Rainy	Rainy	After Rainy	All Seasons
Rats Observed					
Males	13	22	63	55	153
Females	5	12	48	37	102
Total	18	34	111	92	255
Percent Sexually Mature					
Males	100.0	91.0	41.3	74.5	65.3
Females	100.0	75.0	81.3	75.6	79.5
Percent Lactating					
Females	80.0	41.7	69.0	19.0	38.3
Midpoint for Sexual Maturity					
Males	50 g	70 g	103 g	67 g	77 g
Females	90 g	68 g	57 g	60 g	60 g

maturity. In the rainy season a large number of immatures occur in the population and the maturity midpoint increases denoting a rapid increase in individual size. The data for rats captured after the rainy season are similar to the dry season thus giving continuity to the cycle. The females show the same correlations mentioned for the males with the exception of the sexual maturity midpoints.

The data from individual growth show that about two months after birth the rats attain sexual maturity (Table IX) in both sexes.

From Table IX and Figure 5, it can be deduced that the average weight is influenced by season (presumably through food supply) and by the number of young individuals in the population.

Summary

The general purpose of a study of Roof Rats (*Rattus rattus*) was to consider the correlation of seasonal fluctuations of the habitat on the rat population in respect to the population size, distribution, growth, movement, and probabilities of survival in an insular population in Venezuela. Zorro Island has an area of 6.5 hectares and is

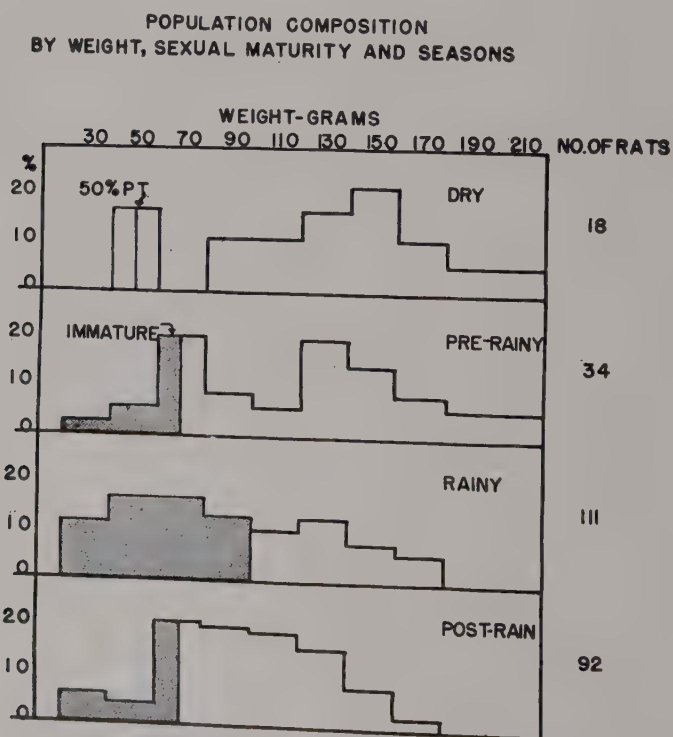


Fig. 5.—Composition of population in various seasons.

separated from the nearest shore by a distance of 750 meters. Its abrupt terrain is covered by a dense tropical deciduous seasonal forest. Besides the rats, other mammals found are bats and occasionally opossums. A great variety of birds and reptiles completes the fauna. The conclusions are based on the observations obtained from the systematic capture, marking, and release of individuals during a period of two years. A total of 153 different rats, 89 males and 64 females, were observed 327 times. No difference was noted between the trapability of males and females. Although the individual growth rate of the rats varies according to season, the average for both sexes ranges from 38 grams during the first month to 15 grams per month during the period between 3 and 6 months.

Great seasonal changes affect the environment; maximum rainfall occurs in August reaching a monthly precipitation of about 200 mm, while during the first three months of the year there is slight or no rainfall. The temperature and humidity do not suffer such extreme fluctuations. These changes presumably produce unevenness in the supply and distribution of food, thus creating marked seasonal variations in the characteristics of the ecosystem's biotic components.

During the rainy season the number of rats reached a maximum of about 40 on the island, later declining to about 10 at the end of the dry season. These individuals are not evenly distributed over the island. Furthermore the distribution also varies according to the supply of food and shelter. Immigration occurs on rare occasions, but emigration is unlikely due to local conditions. Individual movement appears greater for the males than for the females. During the dry season only sexually mature rats were observed but during the rainy season many immatures are present. Breeding occurs throughout the year. Sexual maturity is reached at a weight of about 70 grams and at an age varying from 1.5 to 2.5 months.

The life expectancy appears to be influenced by the relation of the month of birth to the seasons. Rats born in the dry season survived through the wet period but few born in the wet season survived through the dry. Although some rats were observed during periods as long as 15 months the average life expectancy is about 5 months.

REFERENCE

DAVIS, DAVID E. 1956. *Manual for the Analysis of Rodent Populations.* Ann Arbor: Edwards Bros. 82 pp.

A Study of the Population of Insects Emerging as Adults from South Walker Pond at London, Ontario[1]

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During the summer of 1956 a study was undertaken of the population of insects emerging as adults from South Walker Pond near London, Ontario. This pond is one of a group of three "kettle lakes" situated just south of London in Westminster Township and lying just to the northeast of the corner of Wellington Road and the road separating Concession 1 from Concession 2 of the Township. The three ponds are together designated as "The Ponds" by Saunders and Dale (1933) and as "Walker Ponds" on the maps of the National Topographic Series. The most easterly pond is "Spettigues' Pond," the most westerly one is "Saunders' Pond" and the most southerly one is "South Pond" or South Walker Pond. South Walker Pond (Fig. 1) is about 800 feet wide in the east-west direction and 800 feet in the north-south direction with three large bays extending easterly, westerly and southerly from the center of the lake. In the summer of 1956 there was no submerged or floating vegetation on the pond and the bottom was covered with the soft, brown remains of disintegrating leaves. The whole shore of the pond is surrounded by a deciduous wood which is most extensive towards the southeast.

Acknowledgment.—The writer is grateful to Mr. R. B. Catalan who aided daily during the summer of 1956 in collecting insects and in recording data. The Western Ontario Fish and Game Protective Association, on whose property South Walker is located, kindly granted permission for the study of the pond to be undertaken and supplied a boat, wharfing facilities and storage space during 1956.

Methods

Insects were trapped in a floating tent-trap set out on the water at each of five collection sites (Fig. 1). The trap was of the type described by Judd (1957), built to enclose four square feet of water surface. The trap was kept in one position during the course of the investigation and was held there by a rope anchored at one end to bricks on the bottom of the pond and stapled at the other end to the side of the trap.

The pond was completely covered with ice during 1956 until April 5. After that date thawing occurred and by April 10 the whole pond was free of ice. On April 10, the five traps were anchored in position, No. 1 one hundred and twenty feet from the north shore on

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[1] Contribution from the Department of Zoology, University of Western Ontario; a project supported by funds from the Ontario Research Foundation.

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water 23 feet deep, No. 2 fifteen feet from the west shore on water 5 feet deep, No. 3 twenty-four feet from the east shore on water 15 feet deep, No. 4 twenty-four feet from the south shore on water 5 feet deep and No. 5 one hundred and twenty feet from the southeast shore on water 24 feet deep (Fig. 1).

Each day the insects caught in each trap were collected. One side of the trap was raised above the surface of the water and an aspirator was passed into the trap and small insects were sucked into it. Larger insects, such as damsel flies, were picked from the lower surface of the screen of the trap with the fingers. The insects so collected were put into a killing jar and taken to the laboratory for sorting, counting, pinning (or preserving in fluid) and labelling. The depth of the water at each trap was measured each day and the maximum and minimum temperatures of the water for the previous 24-hour period at the bottom were taken at each trap with a Taylor Six's maximum-minimum thermometer. The thermometer was attached to the trap by a rope and was drawn up to the surface to be read. The traps were removed from the water and the last readings of temperature and depth were recorded on November 3.

The various groups of insects were identified by the following taxonomists who, unless otherwise noted, are or were staff members of the Entomology Research Division, United States Department of

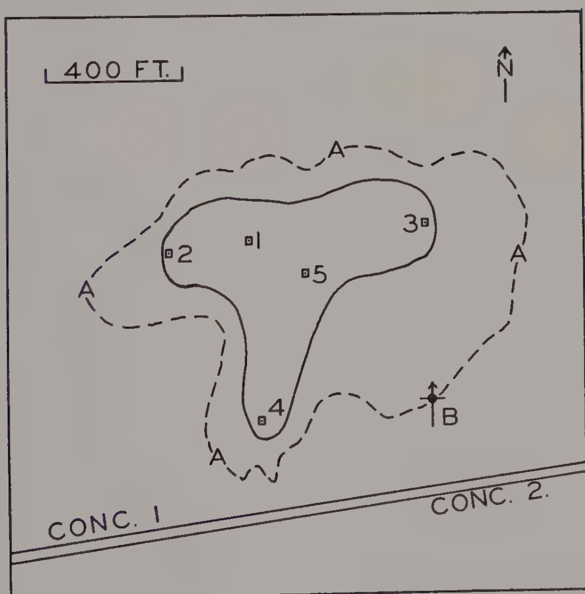

Fig. 1.—Map of South Walker Pond showing location of the five tent-traps (1-5). A—A: outer limit of deciduous wood. B: location of co-ordinate point 42° 57′ 45″ N, 80° 13′ W.

Agriculture: C. P. Alexander, University of Massachusetts (Tipulidae), R. S. Beal (Bruchidae), R. H. Foote (Dolichopodidae, Empididiae, Itonididae), F. P. Ide, University of Toronto (Ephemeroptera), C. F. W. Muesebeck (Braconidae), J. G. Rozen (Anthicidae, Dascyllidae), C. W. Sabrosky (Milichiidae, Sphaeroceridae), R. I. Sailer (Hemiptera), A. Stone (Culicidae, Psychodidae, Scatopsidae), G. B. Vogt (Chrysomelidae), E. M. Walker, Royal Ontario Museum, Toronto, Ontario (Odonata), R. E. Warner (Curculionidae), G. B. Wiggins, Royal Ontario Museum (Trichoptera), W. W. Wirth (Drosophilidae, Ephydridae, Heleidae, Tendipedidae).

All specimens are retained in the collections of the Department of Zoology, University of Western Ontario except as noted (USNM—United States National Museum; ROM—Royal Ontario Museum) in the following account.

PHYSICAL DATA

The measurements of temperature and water depth at the five traps were as follows:

Trap	Day-degrees by Nov. 3	Average Temperature Maximum — °C	Maximum Depth May 15 (inches)	Minimum Depth August 4 (inches)
1	1087	6.1 (October 22)	305	257
2	3390	24.5 (August 20)	92	44
3	3431	25.0 (August 15)	209	161
4	3591	25.6 (June 23)	99	51
5	1133	6.7 (July 17)	317	273

The depth of the water fluctuated equally at the five traps. After the melting of the ice the depth fell a few inches until April 27 (Fig. 2a). After this date continued melting of snow and the onset of spring rains caused the depth to increase steadily to a maximum on May 15 (Fig. 2a). Then the depth decreased until the middle of June and thereafter fluctuated only a few inches through the rest of the season, with minimum depths occurring on August 4.

The maximum and minimum temperatures on the bottom at each trap over each 24-hour period were averaged and the averages for each day were tabulated. The total accumulation of day-degrees at each cage was derived by summing these average temperatures from April 12 to November 3. These accumulations are included in the table above and are shown graphically in Fig. 2c. The accumulations at Traps 2, 3 and 4 all exceeded 3000 day-degrees and are comparable to the accumulations found in the Dundas Marsh in shallow water by Judd (1953). The accumulations at Traps 1 and 5 were much less, owing to the establishment of a thermocline in the pond. Temperature readings taken at various depths from the surface downward near Trap 5 on October 6 showed the epilimnion extending down to 12 feet, the thermocline extending from 12 feet to 21 feet

and the hypolimnion below 21 feet (Fig. 3). Thus Traps 1 and 5 were set over water including the hypolimnion and Traps 2, 3 and 4 over water above the hypolimnion. The average daily temperatures at Traps 2, 3, and 4 increased gradually during the season to values above 24°C (Fig. 2b) and remained fairly constant through June, July and August and decreased gradually in the fall. The temperature at Traps 1 and 5 increased very slightly during May and remained below 7°C during the season (Fig. 2b).

ACCOUNT OF TOTAL CATCH

The numbers of the various insects collected in the traps are presented in Table I and the numbers of insects in the seven orders collected are presented in Table II. During the whole period that the traps were in operation, April 10 to November 3, 4,108 insects were trapped. Most of the insects are species whose larvae or nymphs live

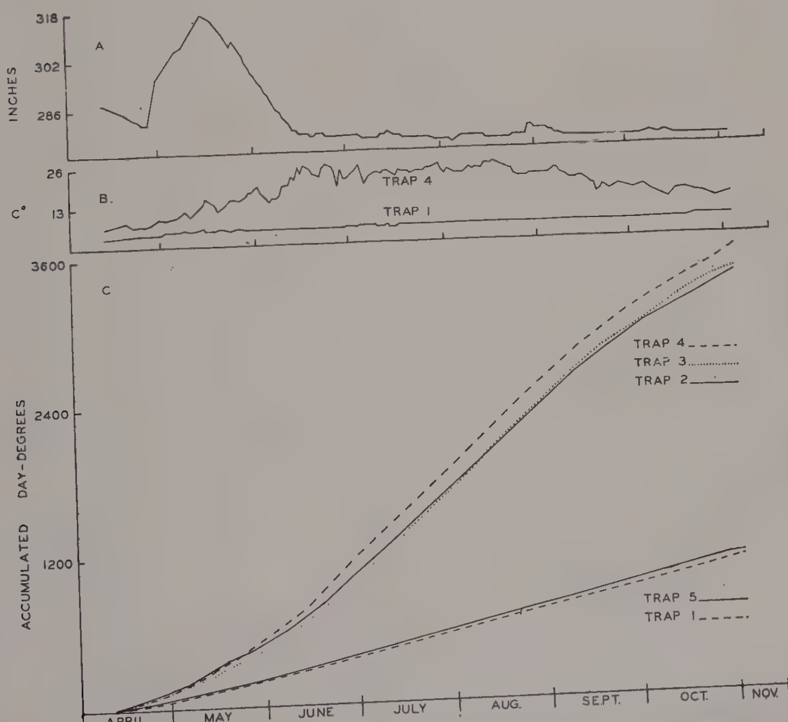

Fig. 2.—A. Water depth at Trap 5.—B. Average water temperature at bottom of pond at locations of Traps 1 and 4. C. Accumulated day-degrees at the bottom at locations of the five traps.

submerged and whose adults emerge from the water, but a few are insects that dwell on aquatic vegetation. The great majority (97%) were Diptera and among these the Tendipedidae predominated (82.5%). Next in point of numbers (15.8%) were the Culicidae. The other families of Diptera and the other orders were present in much smaller numbers.

The most productive sites were at Traps 3 and 4, yielding more than half the total catch. The area of water surface covered by each trap was 4 sq. ft., so the total area from which insects were collected was five times this area, 20 sq. ft. Over the whole season, 4,108 insects were trapped, a yield of 205.4 insects per sq. ft. The first insects emerged on May 4 and the last on October 22 (Fig. 4). The maximum peak of emergence occurred on June 7 (74 insects) owing largely to a big emergence of *Cricotopus bicinctus* (Fig. 5). Three other peaks of emergence occurred on July 11 (64 insects), August 14 (62 insects) and September 7 (65 insects). The catch decreased considerably in October. The distribution of species with respect to the hypo-

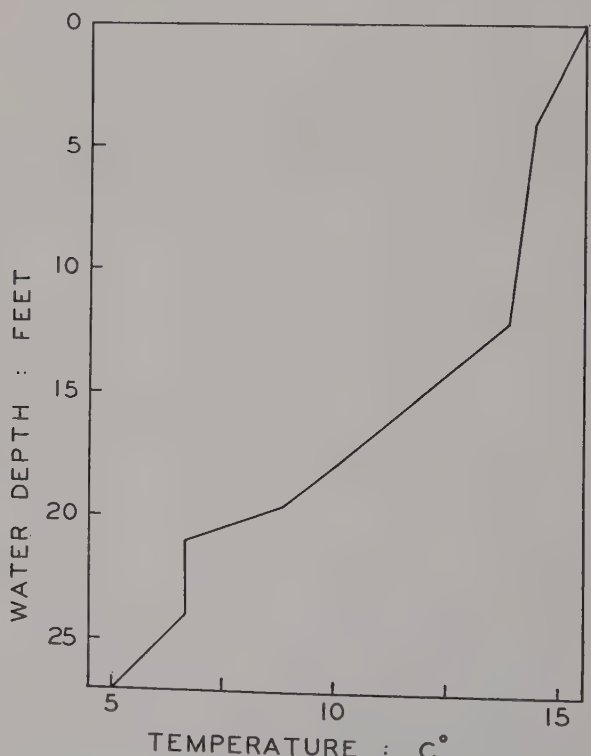

Fig. 3.—Temperature profile of water of pond on October 6 near Trap 5.

TABLE I: Numbers of insects collected in traps

	Trap 1 No.	Trap 1 %	Trap 2 No.	Trap 2 %	Trap 3 No.	Trap 3 %	Trap 4 No.	Trap 4 %	Trap 5 No.	Trap 5 %	Total
EPHEMEROPTERA											
BAETIDAE											
Callibaetis ferrugineus	0	0	0	0	0	0	2	100	0	0	2
Baetis pygmaeus	7	19	1	3	13	32	11	29	6	17	38
Caenis sp.	0	0	0	0	1	100	0	0	0	0	1
ODONATA											
COENAGRIIDAE											
Enallagma vesperum	0	0	0	0	0	0	1	100	0	0	1
TRICHOPTERA											
PSYCHOMYIIDAE											
Polycentropus cinereus	2	5	6	13	22	48	12	25	4	9	46
Polycentropus (?interruptus)	0	0	0	0	3	100	0	0	0	0	3
Nyctiophylax vestitus	0	0	0	0	1	33	2	67	0	0	3
HYDROPSYCHIDAE											
Hydropsyche (?simulans)	0	0	1	33	0	0	0	0	2	67	3
Cheumatopsyche sp.	1	7	0	0	4	3	8	62	0	0	13
LEPTOCERIDAE											
Oecetis inconspicua	0	0	0	0	2	50	2	50	0	0	4
Oecetis cinerascens	0	0	0	0	0	0	1	100	0	0	1
HEMIPTERA											
SALDIDAE											
Saldula confluenta	0	0	0	0	0	0	1	100	0	0	1
MESOVELIIDAE											
Mesovelia mulsanti	0	0	0	0	1	33	0	0	2	67	3
COLEOPTERA											
DASCYLLIDAE											
Ectopria sp.	0	0	0	0	0	0	2	100	0	0	2
CHRYSOMELIDAE											
Longitarsus sp.	0	0	1	100	0	0	0	0	0	0	1
ANTHICIDAE											
Notoxus sp.	0	0	0	0	0	0	0	0	1	100	1
BRUCHIDAE											
Bruchus brachialis	1	100	0	0	0	0	0	0	0	0	1

TABLE I.—(*continued*)

	Trap 1 No.	%	Trap 2 No.	%	Trap 3 No.	%	Trap 4 No.	%	Trap 5 No.	%	Total
CURCULIONIDAE											
Calendra sp.	0	0	0	0	0	0	1	100	0	0	1
DIPTERA											
TIPULIDAE											
Limonia canadensis	0	0	1	100	0	0	0	0	0	0	1
Helius flavipes	0	0	0	0	1	100	0	0	0	0	1
PSYCHODIDAE											
Psychoda lativentris	0	0	2	100	0	0	0	0	0	0	2
TENDIPEDIDAE											
Pentaneura monilis	3	1.5	40	17	62	27	125	54	1	0.5	231
Pentaneura sp.	9	12	14	18	10	12	21	26	26	32	80
Pelopia stellata	0	0	3	21	6	43	4	29	1	7	14
Clinotanypus thoracicus	0	0	0	0	0	0	5	100	0	0	5
Anatopynia dyari	1	100	0	0	0	0	0	0	0	0	1
Procladius culiciformis	32	8	73	20	70	20	142	39	46	13	363
Procladius bellus	10	8	23	15	25	15	72	50	14	12	144
Hydrobaenus sp.	2	10	1	4	16	76	2	10	0	0	21
Cricotopus trifasciatus	1	33	0	0	0	0	1	34	1	33	3
Cricotopus bicinctus	28	13	0	0	62	28	7	3	124	56	221
Microtendipes pedellus	0	0	10	8	85	66	22	17	11	9	128
Polypedilum sp.	4	5	11	20	30	50	12	20	4	5	61
Tanytarsus nigricans	82	18	47	11	191	42	79	17	54	12	453
Tendipes dux	0	0	0	0	0	0	5	100	0	0	5
Tanytarsus punctipes	0	0	4	6	35	63	11	20	6	11	56
Tendipes nervosus	56	66	25	30	4	4	0	0	0	0	85
Tendipes riparius	0	0	0	0	1	17	5	83	0	0	6
Glyptotendipes lobiferus	9	6	14	11	60	47	44	34	3	2	130
Glyptotendipes brachialis	0	0	0	0	7	100	0	0	0	0	7

TABLE I.—(*continued*)

	Trap 1		Trap 2		Trap 3		Trap 4		Trap 5		
	No.	%	No.	%	No.	%	No.	%	No.	%	Total
Stenochironomus hilaris	0	0	0	0	73	75	24	25	0	0	97
Calopsectra sp.	15	1	158	13	489	42	446	38	67	6	1,175
HELEIDAE											
Atrichopogon sp.	2	9	2	9	11	44	4	19	4	19	23
Bezzia glabra	2	13	5	34	2	13	6	40	0	0	15
Bezzia sp.	0	0	2	40	2	40	1	20	0	0	5
Culicoides piliferus	0	0	3	60	1	20	0	0	1	20	5
Palpomyia slossonae	0	0	0	0	1	100	0	0	0	0	1
CULICIDAE											
Chaoborus punctipennis	73	13	68	12	130	24	130	24	150	27	551
Chaoborus flavicans	32	43	7	10	9	12	5	8	20	27	73
ITONIDIDAE											
Itonidini	0	0	3	100	0	0	0	0	0	0	3
SCATOPSIDAE											
Scatopse fuscipes	0	0	1	100	0	0	0	0	0	0	1
DOLICHOPODIDAE											
Dolichopus sp.	0	0	0	0	2	100	0	0	0	0	2
Tachytrecha sp.	0	0	0	0	0	0	1	100	0	0	1
EMPIDIDAE											
Tachypeza sp.	0	0	0	0	0	0	1	100	0	0	1
EPHYDRIDAE											
Hydrellia sp.	0	0	3	60	1	20	0	0	1	20	5
Scatella picea	0	0	0	0	2	66	0	0	1	34	3
SPHAEROCERIDAE											
Leptocera wheeleri	0	0	0	0	0	0	0	0	1	100	1
DROSOPHILIDAE											
Drosophila melanogaster	0	0	0	0	0	0	1	100	0	0	1
MILICHIIDAE											
Desmometopa sordida	0	0	0	0	0	0	1	100	0	0	1
HYMENOPTERA											
BRACONIDAE											
Apanteles plathypenae	0	0	0	0	0	0	0	0	1	100	1
TOTALS	372	9	529	13	1,435	35	1,220	30	552	13	4,108

TABLE II: Number of insects of the seven orders collected in the traps

Group	Trap 1 No.	Trap 1 %	Trap 2 No.	Trap 2 %	Trap 3 No.	Trap 3 %	Trap 4 No.	Trap 4 %	Trap 5 No.	Trap 5 %	No.	% of Diptera	No.	% of Total
EPHEMEROPTERA	7	17	1	2	14	34	13	32	6	15			41	0.99
ODONATA	0	0	0	0	0	0	1	100	0	0			1	0.02
TRICHOPTERA	3	4	7	10	32	44	25	34	6	8			73	1.77
HEMIPTERA	0	0	0	0	1	25	1	25	2	50			4	0.08
COLEOPTERA	1	17	1	16	0	0	3	50	1	17			6	0.12
DIPTERA														
Tipulidae	0	0	1	50	1	50	0	0	0	0	2	0.05		
Psychodidae	0	0	2	100	0	0	0	0	0	0	2	0.05		
Tendipedidae	252	8	423	13	1,226	37	1,027	31	358	11	3,286	82.5		
Heleidae	4	8	12	25	17	35	11	22	5	10	49	1.2		
Culicidae	105	17	75	12	139	22	135	22	170	27	624	15.8		
Itonididae	0	0	3	100	0	0	0	0	0	0	3	0.07		
Scatopsidae	0	0	1	100	0	0	0	0	0	0	1	0.03		
Dolichopodidae	0	0	0	0	2	67	1	33	0	0	3	0.07		
Empididae	0	0	0	0	0	0	1	100	0	0	1	0.03		
Ephydridae	0	0	3	37	3	37	0	0	2	26	8	0.2		
Sphaeroceridae	0	0	0	0	0	0	0	0	1	100	1	0.03		
Drosophilidae	0	0	0	0	0	0	1	100	0	0	1	0.03		
Milichiidae	0	0	0	0	0	0	1	100	0	0	1	0.03		
Total Diptera	361	9	520	13	1,388	35	1,177	30	536	13	3,982	100.0	3,982	97.00
HYMENOPTERA	0	0	0	0	0	0	0	0	1	100			1	0.02
TOTALS	372	9	529	13	1,435	35	1,220	30	552	13			4,108	100.00

limnion (excluding Coleoptera, Hemiptera, Hymenoptera, Sphaeroceridae, Drosophilidae and Milichiidae) is as follows:

1. In hypolimnion:
   Anatopynia dyari

2. Mostly in hypolimnion:
   Cricotopus bicinctus

3. Mostly above hypolimnion:
   Pentaneura monilis
   Pelopia stellata
   Microtendipes pedellus
   Tanytarsus punctipes
   Glyptotendipes lobiferus

4. Above hypolimnion:
   Callibaetis ferrugineus
   Caenis sp.
   Enallagma vesperum
   Nyctiophylax vestitus
   Oecetis inconspicua
   Limonia canadensis
   Helius flavipes
   Psychoda lativentris
   Clinotanypus thoracicus
   Tendipes dux
   Tendipes riparius
   Glyptotendipes brachialis
   Stenochironomus hilaris
   Palpomyia slossonae
   Scatopse fuscipes
   Dolichopus sp.
   Tachytrecha sp.
   Tachypeza sp.

All other species were well distributed above and within the hypolimnion.

ACCOUNT OF SPECIES COLLECTED

EPHEMEROPTERA

BAETIDAE

Callibaetis ferrugineus Walsh.—2 mayflies (Trap 4: July 21, August 1).

Baetis pygmaeus Hagen—38 ♀♀ (Fig. 4) June 15-September 5, maximum July 7 (9 insects). *B. pygmaeus* is recorded from Ontario by Needham *et al.* (1935).

Caenis sp.—1 mayfly (Trap 3: August 19).

ODONATA

COENAGRIIDAE

Enallagma vesperum Calvert.—1 damsel fly (Trap 4: June 24). *E. vesperum* has been recorded from Ontario by Whitehouse (1948). The date of emergence of the specimen from South Walker Pond falls within the period, June 18-August 30, which Whitehouse records as the flight period of this species.

TRICHOPTERA

PSYCHOMYIIDAE

Polycentropus cinereus Hagen.—10 ♂♂, 36 ♀♀ (ROM) (Fig. 4) June 10—September 5, maxima June 12, August 14, (4, 4 insects). Ross (1944) records this species from Ontario.

Polycentropus (? *interruptus* Banks).—3 ♀♀ (ROM) Trap 3: August 14—1, August 16—2).

Nyctiophylax vestitus (Hagen).—3 caddisflies (ROM) (Trap 3: June 26—1 ♂; Trap 4: August 18—1 ♀, August 25—1 ♂). Ross (1944) records this

species from Ontario and gives its time of emergence as May to September, a period which includes the dates of emergence from South Walker Pond.

HYDROPSYCHIDAE

Hydropsyche (? *simulans* Ross).—3 caddisflies (ROM) (Trap 2: July 7—1; Trap 5: July 3—1 ♀, August 13—1 ♀).

Cheumatopsyche sp. (near *campyla* Ross).—13 ♀ ♀ (ROM) (Fig. 4) June 9-August 26.

LEPTOCERIDAE

Oecetis inconspicua (Walker).—4 caddisflies (ROM) (Trap 3: July 28—1 ♀, July 29—1 ♀; Trap 4: July 5—1 ♂, August 7—1 ♂). Ross (1944) records this species from Ontario and gives its time of emergence as May to October, a

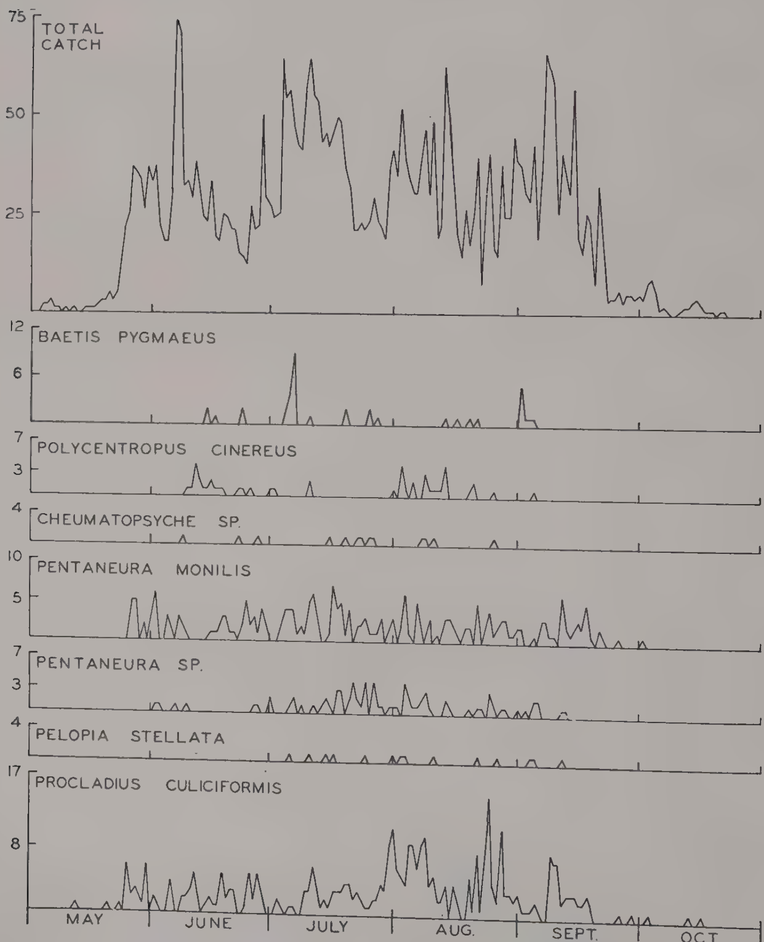

Fig. 4.—Periods of emergence of adult insects.

period which includes the dates of emergence from South Walker Pond.

Oecetis cinerascens (Hagen).—1 caddisfly (ROM) (Trap 4: July 25). Ross (1944) records this species from Ontario.

HEMIPTERA

SALDIDAE

Saldula confluenta (Say).—1 shore bug (USNM) (Trap 4: August 31) This species was previously collected at London by Judd (1957).

MESOVELIIDAE

Mesovelia mulsanti bisignata Uhler.—3 bugs (1, USNM) (Trap 3: September 7—1; Trap 5: August 9—1, August 24—1). This species was previously collected in August at London by Judd (1957).

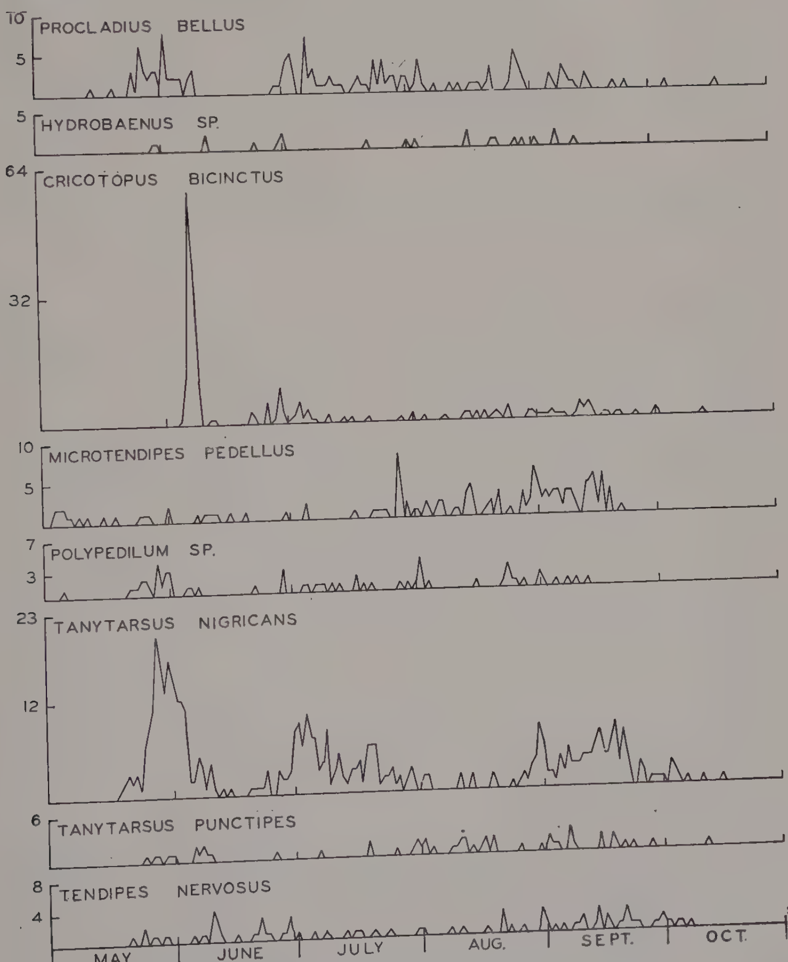

Fig. 5.—Periods of emergence of adult insects.

COLEOPTERA

DASCYLLIDAE

Ectopria sp.—2 beetles (Trap 4: July 8, 17). Blatchley (1910) records that some species of this genus occur in water.

CHRYSOMELIDAE

Longitarsus sp.—1 beetle (Trap 2: August 29). Berg (1949), McGaha (1952) and Usinger *et al.* (1952, 1956) record various chrysomelid beetles as occurring on aquatic vegetation, not including *Longitarsus.* Blatchley (1910) reports that species of *Longitarsus* occur on vegetation.

ANTHICIDAE

Notoxus sp.—1 beetle (Trap 5—July 14). Blatchley (1910) records various species of *Notoxus* as occurring on vegetation about lakes and marshes.

BRUCHIDAE

Bruchus brachialis Fahr.—1 beetle (Trap 1: August 29). Blatchley (1910) records this species from several terrestrial plants. The specimen caught in the trap may have been washed beneath the trap and survived to crawl up into it.

CURCULIONIDAE

Calendra sp.—1 beetle (Trap 4: July 3). McGaha (1952) records several weevils, not in the genus *Calendra,* as feeding on aquatic plants. Usinger *et al.* (1952) record some beetles in the subfamily Calendrinae as being aquatic or semiaquatic.

DIPTERA

TIPULIDAE

Limonia canadensis (Westwood).—1 cranefly (Trap 2: September 11).

Helius flavipes (Macquart).—1 cranefly (Trap 3: August 7). This species was trapped in the Dundas Marsh in Ontario by Judd (1953).

PSYCHODIDAE

Psychoda lativentris Berden.—2 flies (Trap 2: May 30, 31). Johannsen (1934) records several species of *Psychoda* as being aquatic in their larval stage and Judd (1958) records trapping *P. alternata* on the Byron Bog at London.

TENDIPEDIDAE

Pentaneura monilis (L.)—96 ♂ ♂, 135 ♀ ♀ (3, USNM) (Fig. 4) (May 27-October 2, maxima June 2, July 12, August 4 (6, 6, 6 insects). This species was trapped in the Dundas Marsh by Judd (1953).

Pentaneura sp.—80 midges (8, USNM) (Fig. 4) June 2-September 13, maximum July 27 (4 insects).

Pelopia stellata (Coq.)—2 ♂ ♂, 12 ♀ ♀ (1, USNM) (Fig. 4) (July 6- September 12).

Clinotanypus thoracicus (Lw).—1 ♂, 4 ♀ ♀ (4, USNM) (Trap 4: June 23—1 ♂, June 25, 27, July 2, 6—4 ♀ ♀).

Anatopynia dyari (Coq.).—1 ♂ (Trap 1: June 25). This species was trapped by Judd (1957) in June at London.

Procladius culiciformis (L.)—145 ♂ ♂, 218 ♀ ♀ (4, USNM) (Fig. 4) May 18-October 16, maximum August 25 (15 insects). This species was also trapped in the Dundas Marsh and at London by Judd (1953, 1957). In South Walker Pond it occurred above and within the hypolimnion as in Costello Lake, Algonquin Park (Miller, 1941).

P. bellus (L.).—71 ♂ ♂, 73 ♀ ♀ (2, USNM) (Fig. 5) May 15-October 17, maxima June 8, July 7, August 28, (8, 5, 5, insects). This species was trapped also in the Dundas Marsh and at London by Judd (1953, 1957).

Hydrobaenus spp.—21♀♀ (Fig. 5) May 30-September 12.

Cricotopus bicinctus (Meigen).— 127♂♂, 94♀♀ (2, USNM) (Fig. 5) June 1-October 13, maximum June 7 (58 insects). This species was trapped at London by Judd (1957) where the time of maximum emergence was close to that at South Walker Pond. In South Walker Pond these midges emerged mostly from below the thermocline, as was the case in Costello Lake (Miller, 1941).

C. trifasciatus (Panzer).—3♀♀ (1, USNM) (Trap 1: May 27—1; Trap 3: June 2—1; Trap 5: May 31—1). This species was trapped in the Dundas Marsh by Judd (1953).

Microtendipes pedellus (DeGeer) var. *stygius* Townes.—96♂♂, 32♀♀ (2, USNM) (Fig. 5) May 4-September 22, maxima July 27, August 31 (8, 6 insects). This species is recorded from Ontario by Townes (1945).

Polypedilum sp.—34♂♂, 27♀♀ (Fig. 5) May 6-September 13.

Tanytarsus nigricans (Joh.) 237♂♂, 216♀♀ (2, USNM) (Fig. 5) May 19-October 16, maxima May 28, July 4, September 19 (20, 10, 8 insects). This species was trapped in the Dundas Marsh and at London by Judd (1953, 1957).

T. punctipes (Wied.)—56♀♀ (4, USNM) (Fig. 5) May 25-October 22.

Tendipes dux (Joh.).—5♂♂ (2, USNM) (Trap 4: July 7—1, July 10—3, July 12—1). This species was trapped also at London and in the Byron Bog (Judd, 1957, 1958).

T. nervosus (Staeger).—38♂♂, 47♀♀ (2, USNM) (Fig. 5) May 21-October 7. This species was trapped also in the Byron Bog (Judd, 1958).

T. riparius (Meigen).—3♂♂, 3♀♀ (1, USNM) (Trap 3: August 31—1; Trap 4: July 10, 11, 12, 13, 25—5). This species was trapped also in the Byron Bog (Judd, 1958).

Glyptotendipes lobiferus (Say).—79♂♂, 51♀♀ (3, USNM) (Fig. 6) May 19-September 22, maxima June 8, August 30 (9, 6 insects). This species was trapped in the Dundas Marsh and at London by Judd (1953, 1957).

G. brachialis (Coq.).—4♂♂, 3♀♀ (2, USNM) (Trap 3: June 29—1, July 6—2, July 23—1, September 4—1, September 13—1, September 29—1). This species was trapped also at London by Judd (1957).

Stenochironomus hilaris (Walker).—39♂♂, 58♀♀ (3, USNM) (Fig. 6) June 7-September 6, maximum August 7 (5 insects). This species is recorded from Ontario by Townes (1945).

Calopsectra sp.—468♂♂, 707♀♀ (Fig. 6) May 17-October 22, maxima July 10, September 8 (31, 37 insects). These small, green midges were the most common emergents and occurred throughout the season.

HELEIDAE

Atrichopogon sp.—23 midges (10, USNM) (Fig. 6) June 9-September 8, maximum July 4 (4 insects).

Bezzia glabra (Coq.—15 midges (2, USNM) (Fig. 6) June 29-September 9. This species was also trapped in the Dundas Marsh by Judd (1953).

Bezzia sp.—5 midges (USNM) (Trap 2: June 21—1, July 17—1; Trap 3: June 22—1, August 30—1; Trap 4: June 3—1).

Culicoides piliferus R. and H.—5 midges (4, USNM) (Trap 2: June 3, 5, 9—3; Trap 3: June 1—1; Trap 5: June 12—1). This species has been recorded from the United States (Coher) *et al.*, 1955; Lewis, 1959) but not from Canada (Downes, 1956).

Palpomyia slossonae (Coq.).—1 midge (USNM) (Trap 3: June 5).

CULICIDAE

Chaoborus punctipennis (Say).—140♂♂, 411♀♀ (Fig. 6) June 8-October 21, maxima June 17, July 11, August 11, September 9 (17, 13, 22, 23 insects).

This species was collected at London and at the Byron Bog by Judd (1957, 1958).

C. flavicans (Meigen).—33 ♂ ♂, 40 ♀ ♀ (Fig. 6) June 9-September 13, maximum July 12 (12 insects). This species was collected at London and in the Byron Bog by Judd (1957, 1958).

ITONIDIDAE

Itonidini.—Three flies of this tribe emerged in Trap 2 (June 29—2, July 10—1). Johannsen (1934) records that a number of species of gall-flies form galls on aquatic plants.

SCATOPSIDAE

Scatopse fuscipes Meigen.—1 fly (Trap 2: June 29). Johannsen (1934) records rearing larvae of *Scatopse* from an aquatic habitat.

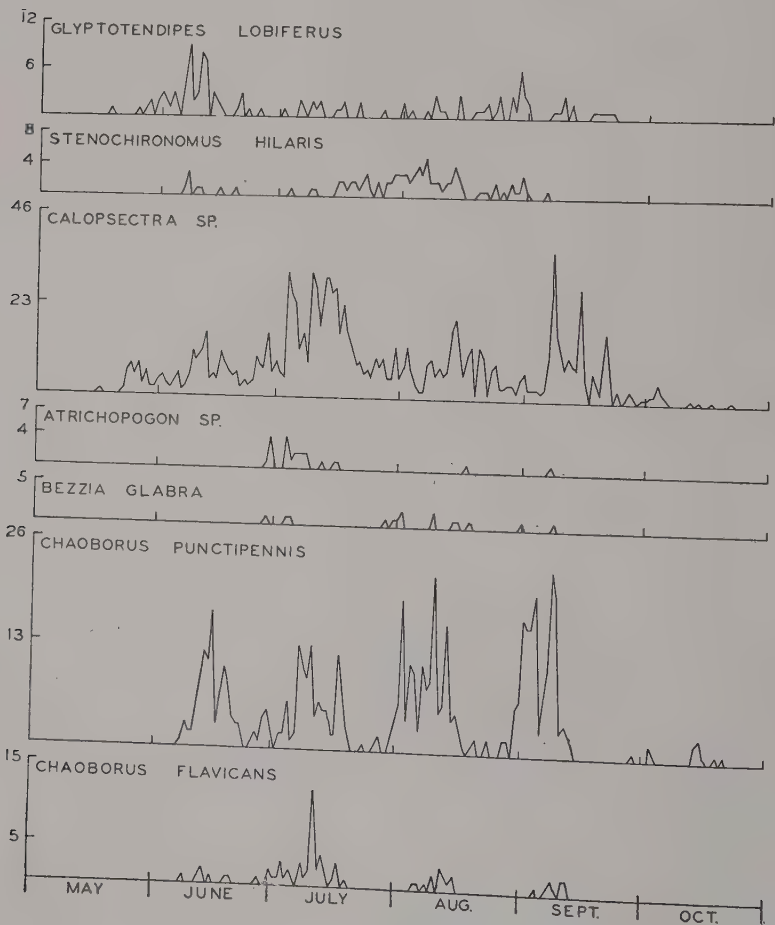

Fig. 6.—Periods of emergence of adult insects.

DOLICHOPODIDAE

Dolichopus sp. (near *monticola* Aldrich).—2 flies (Trap 3: June 17, 22). Several species of *Dolichopus* were trapped in the Dundas Marsh and at London by Judd (1953, 1957).

Tachytrecha sp.—1 fly (Trap: August 27). Usinger *et al.* (1956) record that species of this genus occur along lakes.

EMPIDIDAE

Tachypeza sp.—1 fly (Trap 4: October 8). Usinger *et al.* (1956) list several genera of aquatic Empididae but do not include *Tachypeza.*

EPHYDRIDAE

Hydrellia sp.—5 flies (USNM) (Trap 2: August 21—1, September 6, 12—2; Trap 3: August 31—1; Trap 5: September 8—1).

Scatella picea (Walker).—3 flies (1, USNM) (Trap 3: June 22—2; Trap 5: June 7—1). This species was trapped also in the Dundas Marsh and at London by Judd (1953, 1957).

SPHAEROCERIDAE

Leptocera wheeleri Spuler.—1 fly (USNM) (Trap 5: October 15). Several species of *Leptocera* were trapped in the Dundas Marsh by Judd (1953).

DROSOPHILIDAE

Drosophila melanogaster (Meigen).—1 fly (Trap 4: July 10). *D. quinaria* was trapped in shallow water in the Byron Bog by Judd (1958).

MILICHIIDAE

Desmometopa sordida (Lw.).—1 fly (Trap 4: September 19).

HYMENOPTERA

BRACONIDAE

Apanteles plathypenae Mues.—1 wasp (USNM) (Trap 5: September 10). This species is listed as a parasite of caterpillars (Phalaenidae) by Muesebeck *et al.* (1951). No such caterpillars were collected on the pond but McGaha (1952, 1954) records one species of phalaenid caterpillar which inhabits aquatic plants.

SUMMARY

Between April 10 and November 3, 1956, 4,108 adult insects were trapped in five tent-traps set out on South Walker Pond, two on water over the hypolimnion and three on water not over the hypolimnion. The orders of insects represented were Ephemeroptera (0.99%), Odonata (0.02%), Trichoptera (1.77%), Hemiptera (0.08%), Coleoptera (0.12%), Diptera (97%), and Hymenoptera (0.02%). Midges of the family Tendipedidae constituted 82.5 percent of the Diptera and mosquitoes (Culicidae) 15.8 percent of the Diptera. Other families of Diptera represented were Tipulidae, Psychodidae, Heleidae, Itonididae, Scatopsidae, Dolichopodidae, Empididae, Ephydridae, Sphaeroceridae, Drosophilidae, and Milichiidae. Families of Coleoptera were Dascyllidae, Chrysomelidae, Anthicidae, Bruchidae, and Curculionidae. The numbers and seasonal occurrence, including times of maximum emergence, were recorded for each species. The species were classified according to their relation to the hypolimnion.

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Okinawa's Dry Typhoons[1]

JACK C. ELLIOTT[2] AND YOSHIMA NINO[3]

Tropical storms of typhoon and near typhoon intensities long have been a part of the climatic variabilities of the Ryukyu Islands. Such storms have had a harassing influence on the lives of the people as they have endeavored to wrest a living from the land, keep their homes intact, and fish the in-shore waters. A forty-year summary of climatological records from the Ryukyuan Weather Bureau (1956) indicates that the islands are usually visited by typhoons each year. Most frequently a minimum of three tropical storms, with wind velocities of 65 miles per hour or more, plague the islands each summer. Some years there have been more, some years there have been less, and it is an atypical year when at least one tropical storm of typhoon intensity is not recorded by the Weather Bureau and its effects felt by the people. According to these records typhoons have blown over the Ryukyus every month of the year; however, the usual season is from late July until early October, during the hot, dry period.

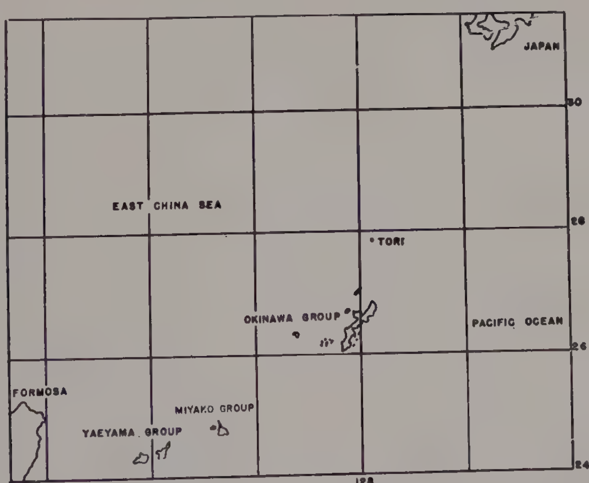

Fig. 1.—The Ryukyu Islands under control of the United States Civil Administration.

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Location, Area, Population

The Ryukyuan Archipelago, composed of numerous islands, islets, and exposed coral reefs, extends nearly 750 miles in a north-easternly direction from a point northeast of Taiwan (Formosa) to near the southern islands of Japan. Yaeyama Gunto (Group), the southern-most one, is just north of latitude 24° N., and the northern-most one, Tori, slightly south of latitude 28° N. The western edge of the island chain is marked by longitude 123° E., the eastern by longitude 132° E. Thus to the west of the major island group is the East China Sea, and to the east the Pacific Ocean (Fig. 1).

Okinawa, the largest island of the chain, covers 64 percent of the total land area. Its southern tip, (Kiyonsaki) is 26°, 5′ N. latitude; north cape (Hedo-saki) 26° 52′ N. latitude, and the 128° meridian of longitude E., passes through the north-central portion.

According to a 1955 population census (United States Civil Administration, 1956) there were 680,905 people living on Okinawa. This figure represents 85 percent of the total population of the Ryukyus. The economy of the island is agricultural, with 55 percent of the total labor force so employed.

1956 Typhoon Season

During the summer of 1956 five typhoons struck the Ryukyu Islands (Table I). Four of these storms hit Okinawa directly, whereas the fifth lashed the island with winds of near typhoon intensity. Although damage to man-made objects was considerable, this paper will discuss only effects of typhoon on vegetation.

Wind and salt-spray damage from the typhoons retarded maturation of most crops, and resulted in near failure in a few instances. Two typhoons ("Wanda" and "Harriet") were "dry" (those during which there is little or no precipitation), and caused considerably more

Table I.—Typhoons affecting Okinawa during the 1956 season

Name of Typhoon	Period Typhoon Within Area of Circle Approximately 240-Mile Radius with Center at Naha				Wind Velocity Recorded at Naha (Miles Per Hour)		Approximate Total Precipitation at Naha During Typhoon Period (Inches)
	Entered		Departed				
	Date	Time	Date	Time	Average	Maximum (Gusts)	
Wanda	7/31	0200	8/1	1900	73	111	8.0
Babs	8/14	1000	8/16	1400	64	94	7.4
Diana	9/1	1100	—	—	35	52	0.32
Emma	9/7	1200	9/9	1100	97	165	15.2
Harriet	9/25	2400	9/26	1800	87	129	3.96

salt-spray burning to crops and natural vegetation than intervening ones, which coincided with considerable rainfall. Although data in Table I are indicative of heavy rains during "Wanda" and "Harriet," a factor not revealed by these data is that rains did not come until the waning hours of the storms, which was too late to wash off wind-blown salt-spray before considerable burning had taken place.

Effect on Natural Vegetation

The zonation of vegetation along the coastal areas, and the effect of salt-spray on that vegetation has held the interest of numerous investigators for many years. Boyce (1954), in reporting the results of an intensive study of the "Salt Spray Community" has reviewed the extensive literature on this subject. In most instances these investigations were carried on in coastal regions where the vegetation has been subjected to long periods of salt-spray depositions and thus reflects the results of actions and reactions over a long time span.

Similar results may be seen reflected in the zonation of coastal vegetation on Okinawa. Ryukyuan Pine (*Pinus luchuensis* Mayr.)[1], common along the coast and on high headlands, is quite asymmetrical, with contorted top, short seaward-side limbs, and long, graceful, landward-side branches (to many a U. S. Serviceman, remindful of the Monterey Pine). Numerous "Shrine forests," composed of pure stands of Sea Hearse (*Hernandia sonora* L.) growing on sandy strand or rocky beach, have a graded stature in both height and girth from strand landwards; those nearest the sea are much misshapen with a definitely asymmetrical growth habit. In the scrub forests located near the sea, the velvet-leaf tree (*Messerschmidia argentea* (L.) Johnst.), which usually has the greatest abundance nearest the shore line, likewise shows the effects of nearly continuous salt-spray depositions by a growth habit peculiar to its ecological niche. Other members of this community which respond in a similar way are Orange Jessamine (*Murraya paniculata* (L.) Jack.), *Macaranga tanarius* (L.) Muell., *Premna obtusifolia* R. Br. and several species of fig (*Ficus*).

However, certain environmental differences are present under typhoon conditions which act and react to produce results that are varied from those produced under normal coastal situations. Noticeable among these differences are: 1) deposition of a high salt concentration over the entire plant body, rather than on the windward side only; 2) the relatively short length of time that these plants are subjected to these critical conditions; 3) the exceedingly high wind velocities, often producing mechanical injury, thus allowing easy entrance of salt solutions. In the first instance a heavy salt concentration quickly covers the aerial portion of the plant. Plasmolytic reactions occur throughout the whole plant body, rather than the more common one-sided reactions produced within coastal environments. Secondly, the

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[1] Nomenclature is that of Sonohara, Sakuya; Shinjun Tawada and Tetsuo Amano. Flora of Okinawa. 1952.

length of time that the plants are subjected to these conditions is variable. Many typhoons are accompanied by heavy rains which serve to wash much of the salt-spray from the plant before severe burning can result. This factor may account, in part, for their speed of recovery if mechanical injuries have not been too extensive. In Okinawa, however, "dry" typhoons are not infrequent. In such instances considerable burning of the vegetation is common and the results are most spectacular, yet devastating. In the third place, the extremely high winds serve to increase and accelerate processes of mechanical injury, thus allowing greater infiltration of salt solutions. These factors combine to produce noticeable dwarfing of the whole plant. Along the coast, where the vegetation is subjected to salt-spray almost continuously, the asymmetrical growth habit is accompanied by dwarfness as result of the influence of many past typhoons.

FORESTED AREAS

The topography of the north-central portion of the island is undulating to hilly, interspersed with broad valleys and small, flat plateaus. Most of the soil of the area is deep, rapidly drained, high in acidity, steep and nonarable. This part of Okinawa, not utilized for agricultural purposes, villages, or U. S. military installations, has a fine stand of young Ryukyuan pine. Strong typhoon winds produced little breakage of limbs, tops, or wind-throw. Gales, however, increased transpiration rates sufficiently to produce some "transpiration burn" with a consequent set-back to developing young shoots. Heavy salt burn (distinguished from "transpiration burn" by complete yellowing of needle-leaves) was a conspicuous feature within the area, with needle-leaves, limbs, and bark showing injury. Some sand-blasting of bark from lower parts of trunks likewise occurred. Numerous mis-shapen trees are certain to result from the effect of these typhoons and susceptibility to diseases will be noticeably increased because of bark injury. Cone and seed production was markedly reduced. Young cones were burned beyond recovery and older, but immature ones were blown from the trees. A high percentage of young seedlings, too short and supple to be much affected by the winds, were killed as a result of salt depositions from the "dry typhoons."

Farther to the north, in the mountainous areas of the islands, the pines are mostly confined to the lower third of the generally steep slopes. Protection afforded by the precipitous areas above the pine zone kept typhoon damage to a minimum, especially within the interior. Stands along the coastal slopes on both the Pacific Ocean and East China Sea were affected in much the same manner as described above. However, that typhoons can do strange things on occasion may be seen from the fact that some of the most severely burned pines were found in what appeared to be well-protected, interior valleys, with no indication from the vegetation around them to suggest probable pathways of approach.

Much of the mountainous area of northern Okinawa supports a broad-leaved, evergreen forest; the "Lauri-silvae" of the Japanese (Walker 1952-1954). During the early years of World War II, the Japanese effected a heavy timber-drain on the area for naval supplies. At the conclusion of the war, the area again was the scene of much lumbering activity in order to supply construction materials for post-war building. Consequently, today, the stands are mostly of coppice development, numerous in stems, small in stature, and frequently much contorted in shape. Large trees are mostly culls, either left from former lumbering operations, or confined to nonaccessible areas. Abundant in this community are "Iju" (*Schima liukiuensis* Nakai) and "Okinawa-shii" (Okinawa chestnut) (*Castanopsis cuspidata* (Thunb.) Schottky) with an admixture of numerous members of the Lauraceae, Ebenaceae, and a lesser representation of other families.

Wind-throw was most evident among the larger and older trees after the passing of the typhoon. Damage to young, immature fruits from limb-rub and wind-whip was common, seriously reducing the year's seed crop. (For example: A seed exchange which had been arranged with the Forestry and Timber Bureau, Commonwealth of Australia for *Schima* had to be postponed until another growing season). Burn from salt-spray was prominent, causing defoliation, as well as death to new growth on the trees. Although regions evidencing greatest injury were generally to be found along the coast, and in coast-facing river valleys, areas of like damage were apparent on the highest mountain (Mount Onna, 636 meters) as well as in some interior depressions, indicating that wind-blown salt-spray was carried completely across the island.

On frequent occasions, especially following the "dry" typhoons, woody species were seen to renew their reproductive cycles following defoliation. The phenomenon appeared most frequent among members of the Moraceae, with individuals of *Morus australis* Poir., for instance, putting forth new catkins and leaves following three "dry" typhoons, before finally succumbing to the vicissitudes of subsequent storms.

Upsets in the life-cycles of vegetation, whether frequent, as is apparently the case in Okinawa because of the effects of numerous typhoons, or seldom, as might be induced by infrequent, catastrophic storms or man's disturbance, are important ecological elements which need to be considered when analyzing the vegetation in any region. This factor is of considerable magnitude when synecological investigations, aute-ecological studies of native species, and planning programs for introduction of new species on Okinawa (or elsewhere) are considered. Costello (1957) has pointed out that: "Disturbances in life cycles are the causes of change in range conditions and productivity, and therefore, the source of many problems in range management." So, also, are they potential sources of problems when not adequately considered as a part of the total ecology of an area.

WILD ("GENYA") LANDS

Nonarable land in the central and southern portion of the island is called "Genya" (Wild) land by the Okinawans. Composed of thin-soiled, steep hills, with local limestone outcrops, it makes up 40 to 45 percent of the area. The principal components of the wild-land vegetation are grasses, especially *Miscanthus floridulus* (Labill.) Warb.; vines, (*Vitis sp., Smilax sp.*); shrub thickets, (*Rosa bracteata* Wendl., *Rubus grayanus* Maxim., *R. sieboldii* Blume., *Rhaphiolepis umbellata* (Thunb.) Makino., *Pittosporum denudatum* Nakai., *Leucaena glauca* (L.) Benth. and in some instances communities of Cycad (*Cycas revoluta* Thunb.), Ryukyuan Pine and small-leaved banyan.

The extensive areas of Sword-grass (*Miscanthus*) are the main source of supply for thatching materials and for the cottage industry of "Panama" hat manufacture. They are, therefore, of considerable importance. Cycad ("Sotetsu") leaves are used for decoration during festivals and celebrations, and the fruits are utilized on occasion of severe food shortage. Most serious damage to the vegetation of the wild-land occurred to the shrub aspect where fruits, used as a part of the diet, were badly bruised from limb-rub and wind-whip, and blown-off, or withered as a result of salt-spray deposition. Considerable defoliation also was produced. Nearly pure stands of "Gingokan" (*Leucaena glauca* (L.) Benth.), a source of charcoal stock and kindling wood, stood gaunt and bare after the effects of the "dry" typhoons and it was several months before new growth became evident. Although there was some browning of leaf and stem, the vegetative portion of the grasses was slightly damaged from salt burning. Flowering, however, was considerably affected, with as much as 70 percent of the area failing to produce the "silver plume" so characteristic of *Miscanthus* during October and November.

The influence of typhoon damage on the vegetation of wild ("Genya") lands is difficult to evaluate. Certainly some loss to the wild fruit crop has much reaction on the supplementary diets, and the beating taken by "Gingokan" prevents it maturing into a very sizeable tree or shrub for firewood or charcoal-stock. Whereas, the vegetative portion of sword grass is little damaged, the loss of flowering and fruiting stages reduces to some degree the extent of new areas for thatching materials. According to Okinawan botanists (Shinjun Tawada, Forestry Section, Department of Natural Resources, Government of the Ryukyuan Islands, and Professor Shunichi Shimabukuro, Dean, Agriculture and Home Economics Division, University of The Ryukyus) the grass aspect of the wild-lands was dominated by Cogon (*Imperata cylindrica* (L.) Beauv.) previous to the war; the establishment of sword grass (*Miscanthus floridulus*) was an aftermath of the devastation which occurred to the central and southern portions of Okinawa. Peculiarities of the edaphic situation would appear to be an important factor in determining the unique nature of the "Genya" land's vegetation. Typhoons have, no doubt, exerted

some influence and selective action, and the prewar abundance of Cogan grass could be related to its apparent typhoon resistance. The long-time influence of man, as well as his more recent greater destruction through war activities, must be acknowledged. Thus it is possible that the present vegetational aspect of the "Genya" lands is, to a greater or lesser degree, one of a successional nature.

EFFECT ON CROPS

Sweet potatoes.—This crop, which occupies the largest planted area of the island and serves as the basic food, was damaged to the greatest extent. Plantings normally made in early July but delayed because of hot, dry weather, were badly burned from the effects of the "dry" typhoon "Wanda," and rendered almost a complete loss by "Babs," two weeks later. Efforts to replant were continued through the arrival of "Harriet" with little success. Thus, three months of the usual growing season were lost to crop production. Numerous plots, established on beach strand, were covered with 3-5 inches of wind-driven sand causing further loss to the total annual production.

At the present time three varieties of sweet potatoes are grown most extensively on Okinawa: Okinawa No. 1, Hijagawa No. 1, and Yaeyama-akago. These varieties are the result of a breeding program carried on by Yogi Agricultural Experiment Station (Government of Ryukyu Islands Institution) since prewar days. Previous to the war, all sweet potato breeding for Japan was carried on by this station as these plants bloom in Okinawa and therefore do not require crossing with Morning Glory (Kohler, 1957). Whereas these varieties are relatively resistant to diseases common to the islands, they all require a six-month growing season, and difficulties can be encountered when the planting time coincides with a typhoon season, as frequently happens. Efforts to secure a suitable stock requiring a shorter growing period are being put forth by the Agricultural Division, University of The Ryukyus and Yogi Experiment Station through importation of likely varieties from other countries. Some success has been obtained with varieties from the state of Louisiana (U.S.A.); however, experiments have not yet reached a stage where plants can be released in abundance to growers. Real promise for a solution to this problem lies in a plant breeding program, still in its early stages, at the several Ryukyuan Government stations and at the University of The Ryukyus. Taking into account the ecological concept of day-length and photoperiodicity, experiments are being conducted in an effort to breed a disease-resistant, high yielding variety, requiring a growing season less than the present six-month one. Success in this program would do much to offset the serious losses experienced with this crop in years of numerous "dry" typhoons; as Nuttonson (1952) has said, "The Ryukyus, already suffering a chronic food deficit, could ill afford to sustain major damage to the sweet potato crop."

Sugar cane.—Greatest damage to this, Okinawa's most important export crop, was from the effects of high wind velocities rather than from burning by salt-spray. Fields of young cane planted in April or July had their foliage leaves and growing points severely damaged with each successive typhoon. In numerous instances, the leaves were completely stripped from the stem, in other situations they were badly torn and shredded, necessitating regeneration with the onset of favorable growing conditions. In plots of older cane, planted the previous year, stalks were blown nearly flat and several weeks were required before they assumed an upright position. Thus, with tillering and lodging of the mature cane, and processes of regeneration necessary in the younger stands, the usual harvest dates were delayed by more than a month. Fortunately the cane could be harvested by the use of the customary hand-sickle, whereas the lodged cane could not have been harvested by mechanical means.

Because of the severity of damage to the cane, the 1956 yields did not exceed those of the 1955 season despite the fact that the 1956 cane acreage had been increased by 20 percent. Further losses to the crop, as a result of typhoon damage, are indicated in harvest reports from the several contrifugal sugar mills. These reports indicate an increase in fiber-content, whereas measured sugar-content decreased from 18 or 19 degrees to 14 or 15 degrees (Kohler, 1957). August and September plantings were delayed because of bad weather and overly wet soils created by the typhoons and their accompanying rains.

Rice.—Typhoon damage to paddy-lands, seed-beds and transplants, which were being readied for the second annual rice crop, resulted in approximately a 20 percent loss when compared with yields of previous years. Most extensive damage came when man-made sea-walls were breached by the surf, thereby permitting inundation, erosion, and sedimentation of paddy-lands. Heavily sedimented areas required reclamation measures before return to cultivation. Most seed-beds were planted following typhoon "Wanda," with transplanting taking place after the passing of "Babs." Heavy rains accompanying the later typhoon flooded many of the seed-beds resulting in suffocation of the plants before the excessive water could be drained off. Additional losses occurred as the result of more suffocation and erosive action during and immediately after typhoon "Emma." Dry "Harriet," the last typhoon of the season, produced some burning. This effect was most evident in narrow valley bottoms along the west coast in the southern part of the island. Here, apparently, narrow valleys, running at right angles to the coast, served as funnels for the winds with their heavy loads of salt-spray. Consequently the upper third of the rice plants in paddy-lands so situated were considerably burned. Inspection of the areas, two weeks after the incident, showed almost complete recovery, however.

Papaya and banana.—There was no crop of papaya (*Carica papaya* L.) fruits on Okinawa in 1956. "Dry" typhoon "Wanda," with

high wind velocities and heavily laden with salt-spray, came upon the plants as the fruits were starting to set, or were in early stages of maturation. Plants not broken off by the typhoon were left standing apparently lifeless; foliage leaves burned and withered, and fruits dangled as dry, shrunken, brown balls. No evidence of renewed growth was apparent in the two weeks elapsing between "Wanda" and "Babs." By September, when "Emma" blew in, new crowns of foliage leaves were beginning to appear. Following "Emma," those plants still standing remained slim, stark, pillars until a flush of new growth started to show during late March and early April, 1957.

Fiber banana plants (*Musa liukiuensis* (Matsum.) Makino.) with their massive, pendant leaves, were blown down, or leaves so badly shredded as to render them useless for the cottage textile industry. Only in a few isolated instances, in deep well protected valleys in northern Okinawa, were these plants spared destruction. The edible banana (*Musa paradisiaca subsp. sapientum* (L.) Kuntz.), a frequent court-yard plant grown for family consumption, suffered a similar fate.

Pineapple.—Although there was little apparent direct damage to pineapple from the typhoons, there was, nevertheless, considerable soil erosion when rains beat down on recently established plots, and rivulets gullied through them from higher areas. Extensive growing of pineapple is comparatively recent in Okinawa (12 acres in 1952, 400 acres in 1956). It is planted on bench-terraced hillsides where formerly grasses, shrubs, and second-growth sprout forests served to prevent serious erosion. Improved terracing methods, with careful thought given to contour shape, are urgently needed, if this phase of Okinawan agriculture is to develop into a long-time, profitable practice.

Commercial gardens.—Growing of fresh vegetables for Quartermaster and wholesale-retail sales has become an important part of the farming activity in the past several years. Because the hot, dry summer months are the "off-season" for this truck-crop, relatively little total loss was experienced. Some damage, however, occurred to the late, unharvested tomatoes, squash, melons, cut-flower stock, etc. Burning from the salt-sprays of "dry Wanda" was a prime factor in the latter instance.

Home gardens.—Decorative plantings around the government buildings, school houses, and the concrete, typhoon resistant homes in the several American Dependent housing areas were greatly affected by typhoon damage. The shrubs: Hibiscus (*Hibiscus rosa-sinensis* L.; *H. syriacus* L.; *H. schizopetalus* (Mast.) Hook, f.; *H. mutabilis* L.); Japanese Privet (*Ligustrum japonicum* Thunb.); Crepe-Myrtle (*Lagerstroemia indica* L.); Seven-colors (*Lantana camara* L.); several species of Bougainvillea (*Bougainvillea spectabilis* Willd., *B. spectabilis var. lateritia* Lam., *B. glabra* Choisy); Blood-flower Milkweed (*Asclepias curassavica* L.) and others were nearly defoliated and their grow-

ing tips badly burned during "dry Wanda." New leaves appeared within a week to ten days; however, the effect of lashing winds and driving rains during later typhoons kept them in a state of retarded growth until several months after the final storm of the season. Broad-leaf evergreen trees: Acacia (*Acacia confusa* Merr.); Coral Tree (*Erythrina variegata var. orientalis* (L.) Merr.); Rosewood (Autumn Maple) (*Bischofia javanica* Blume.); Small-leaved Banyan (*Ficus retusa var. nitida* (Thunb.) King.), used as yard plantings were severely injured. Defoliation and killing of tender, new twigs from salt-spray burn of the first typhoon set the growth of these trees back to such an extent that some failed to recover; others were only starting to show signs of renewed life in December. The needle-leaved trees; Ryukyuan Pine and Australian Pine (*Casuarina equisetifolia* J. & G. Frost) were likewise badly burned from salt-spray and there was considerable deformation from top and limb breaking among the latter species. Vines used for shade and concealment were injured in various ways. Most affected were Morning Glory (*Ipomoea purpurea* Lam.) and *Wisteria floribunda* (Willd.) DC. Flower beds of annuals, biennials and perennials were either burned beyond recovery or washed out by torrential rains, necessitating new plantings with the advent of suitable growing conditions.

Windbreaks.—Effective tree and shrub windbreaks are an important adjunct to Okinawan life. Species must be used which can withstand not only the many typhoons, but also the year-around, more or less steady monsoonal winds as well. Nuttonson (1952) has pointed out that wind velocities of 38 miles an hour or more have been recorded in every month of the year on the island.

Windbreaks for protection to agricultural crops are used most extensively along coastal flats, valley entrances, and on the higher plateaus. Screw-pine (*Pandanus tectorius var. liukiuensis* Warb.) is most commonly used along the coastal flats where it serves the dual purpose of windbreak and sand-binder. Frequently, one or more rows of Australian Pine are planted on the cultivated side of the Screw-Pine in order to give additional height to the windbreak. Australian Pine, along with Alexandrian Laurel (*Calophyllum inophyllum* L.) and Garcinia (*Garcinia spicata* Hook.f.) are more frequent in the other two situations, with the former being the most common. A species of rapid growth, Australian Pine was introduced following the war to replace windbreaks then completely wiped out.

Domestic windbreaks are used around rural homes, villages and towns for protection from winds and to lend some degree of privacy to the open-type dwellings. Tall hedges of Hibiscus (*Hibiscus rosa-sinensis* L.) with groves of Alexandrian Laurel, *Garcinia*, and Australian Pine constitute the more common type. On occasion small and large-leaved banyans (*Ficus retusa var. nitida* (Thunb.) King - *F. superba var. japonica* Miq.) may be found interspersed with the other species. Walker (1952-1954) has described the appearance of these domestic windbreaks as follows: "Most striking among the cultivated

trees in every village is the 'fukugi,' *Garcinia spicata,* a dark-green, thick-leaved introduction from southern Asia, its shape reminding westerners of the lombardy popular. It grows in close rows along the streets and property lines, and, because of its slow growth, one can guess from the size of the 'fukugi' trees the age of the village."

These windbreaks withstood the high wind velocities of the typhoons and their accompanying salt-spray with varying degrees of success. Most resistant was Fukugi. There was little or no breaking of trunk or limbs, and although leaves were badly browned from salt-spray burn, no defoliation occurred. Alexandrian Laurel likewise withstood the storms well, having a minimum of breakage and some defoliation in areas nearest the coast. Australian Pine suffered the most damage, both from high wind velocities and burn from salt-spray. Most of these trees had their young branches killed from the effects of salt depositions and in many instances the upper third of the crown was blown away. Rows of Australian Pine, which before the storms were forty feet or more tall, resembled tall hedges following trimming operations necessary to remove broken tops, side branches and dead portions. Some typhoon damage to Screw-pine windbreaks was evident following the passing of "Emma," the third storm of the year, when they began to look beaten and gray. It is possible, however, that some of this appearance resulted from a picking of fruits and leaves for use as offerings at ancestral tombs during the mid-September Oban ceremony. Hedges of Hibiscus, defoliated during "Wanda" remained naked and gaunt for the remainder of the typhoon season.

Because of the extensive damage to Australian Pine from the typhoons it is apparent that it will be necessary to re-evaluate the use of this species as a common windbreak tree. Whereas resistance to salt-spray burn and wind breakage make *Garcinia* and Alexandrian Laurel desirable species, their slow growth rate reduces their value in early stages of windbreak establishment. Until such time as a satisfactory replacement can be found for Australian Pine it may be feasible to combine Screw-pine with *Garcinia* and Alexandrian Laurel thereby getting some protection from Screw-pine during the period that the other two species are growing large enough to offer protection from the winds.

There is one bright spot, floristically speaking, on the "typhoon horizon" of Okinawa. Thirty-six to forty-eight hours after the passing of a storm, Typhoon (Zephyr) Lilies, — pink (*Zephyranthes grandiflora* Lindl.) and white (*Z. candida* Herb.) —, burst into bloom. Used extensively along approach walks or bed-borders, they are the one bright spot of color in an otherwise black-burned, wind-whipped vegetation, and they seem to beckon to a discouraged people as if to say, take hope, there is yet life in the plants.

SUMMARY

"Dry" typhoons on Okinawa have a deterrent and upsetting effect

on the life cycles of its vegetation. Heavy salt depositions from spray blown from surrounding salt waters serve to: 1) destroy tender growing points, retarding growth; 2) cause considerable defoliation, thus upsetting normal food metabolism processes; 3) set-back formation and development of reproductive processes, reducing supplies of fruits and seeds; and 4) produce an added aspect of asymmetrical growth-form and dwarfness to coastal vegetation. High wind velocities cause damaging effects by: 1) bole and limb breakage; 2) windthrow; 3) wind-whip and limb-rub to fruits; and, 4) transpiration burn, which affects plant-water balances. Typhoons which are not "dry" create the same effects as regards damage from high velocities. In some instances salt burn occurs when the rains do not come in early stages of a typhoon. Typhoons accompanied by torrential rains increase erosion processes and most frequently result in damaging floods to paddy-land and other farming areas.

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Differentiation and Commensalism in Podocoryne carnea[1]

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Podocoryne carnea is a commensal hydroid which attaches as a planula to the shell of a hermit crab. Here the planula metamorphoses into the mature hydranth form, and a colony is produced asexually by means of stolons which grow from the base of the hydranth (Fig. 1). More hydranths develop upon the stolons. Ultimately a colony consisting of three major types of hydranths exists on the hermit crab shell: (1) nutritive hydranths, the feeders, resembling pond hydra; (2) generative hydranths, producing medusae which in turn liberate

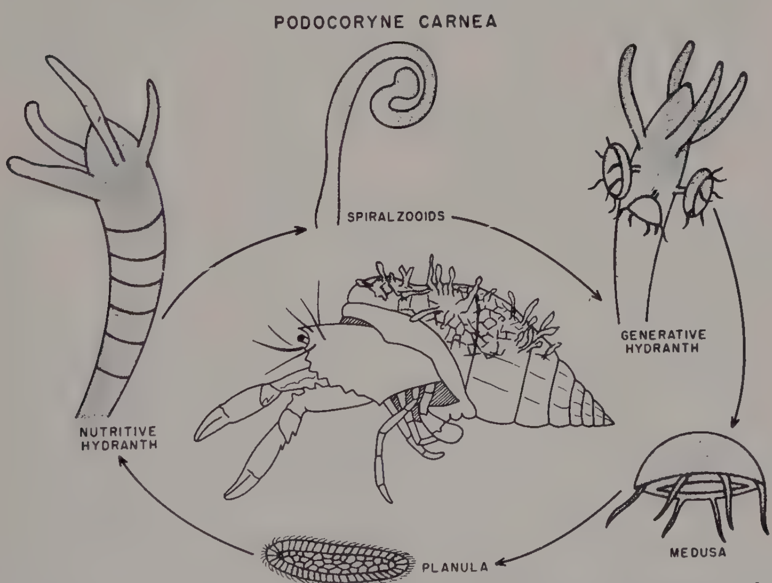

Fig. 1.—Life cycle of *Podocoryne carnea*. The planula settles on a shell occupied by a hermit crab and metamorphoses into a nutritive hydranth. From the base of the hydranth stolons grow, and upon the stolons other hydranths form. Mature, crab borne colonies have a hydranth population consisting of nutritives, generatives, and spiral zooids. Generative hydranths form and release medusae which swim about and discharge gametes into the water. The gametes unite and give rise to the planulae.

[1] This report is based on research supported by Grant G-5542 from the National Science Foundation to S. M. Rose.

gametes; and (3) the spiral zooid, an elongate, filiform hydranth, coiled like a watch spring, which responds to stimulation by a violent uncoiling. It is the commensal nature of spiral zooid genesis with which we are here concerned.

Although colonies can be maintained in the laboratory by transplanting single hydranths to microscope slides, it is notable that only the nutritive and generative hydranths will differentiate on these colonies. The spiral zooid never forms on slide-grown colonies. Also of interest is the fact that on the crab shell spiral zooids appear only around the opening from which the crab emerges. On the basis of these two observations, one may assume that the crab is in some way responsible for the differentiation of spiral zooids. Such an assumption is easily tested. The results, detailed in Table I, substantiate this hypothesis.

Hermit crabs (*Pagurus longicarpus*) were removed from *Nassa trivittata* shells bearing *Podocoryne* colonies by treating the crabs with sea water through which CO_2 had been bubbled.

To one group of shells, maintained as controls, crabs were returned. The other shells, without crabs, comprised the experimental group. Each group was kept in a 4-inch finger bowl partially submerged in the sea table and supplied with constantly running sea water which had been filtered through glass wool.

After 6 days, spiral zooids remained on only one shell in the group of non-inhabited shells. Five days later, when no spiral zooids remained, crabs were returned to a number of these shells. Within 5 more days, all of the shells to which crabs were returned exhibited spiral zooids. Repetition of the experiment with a different group of crabs and shells resulted in a similar loss of spiral zooids from all shells with crabs removed. The shells maintained as controls, containing crabs throughout the experiment, showed no change in spiral zooid population (Fig. 2).

During the first week of the experiment, while spiral zooids were disappearing from the colonies, these zooids were observed in all stages

TABLE I.—Dependence of spiral zooid maintenance on a *Pagurus* supplied factor

	Number of colonies	Colonies with spiral zooids after 10 days		Number of colonies	Spiral zooids reappeared
EXPERIMENT 1					
Crabs removed	29	0	crabs returned	24	24
			crabs not returned	5	0
Crabs present	16	16			
EXPERIMENT 2			Time limitation prevented further verification of the ability of these colonies to form spiral zoooids when crabs are returned.		
Crabs removed	27	3			
Crabs present	6	6			

of their transformation to either nutritive or generative hydranths. The details of this transformation will be reported separately.

Some idea of the nature of the crab's influence upon this differentiation may be gained from the fact that after spiral zooids had disappeared from the colonies, a new type of zooid was seen to arise. This was a small hydranth, devoid of tentacles, with a band of orange pigment proximal to its rounded end. No hypostome could be observed at this end. Within 24 hours of their appearance, such hydranths formed tentacles, and within 3 or 4 days they could not be distinguished from nutritive hydranths. Nutritive hydranths normally display tentacles almost immediately after the hydranths appear as slight swellings on the stolon. This phenomenon would seem to indicate that although colony differentiation is responsible for the appearance of a specialized hydranth type, the crab supplies some factor necessary to spiral zooid maintenance and to subsequent differentiation.

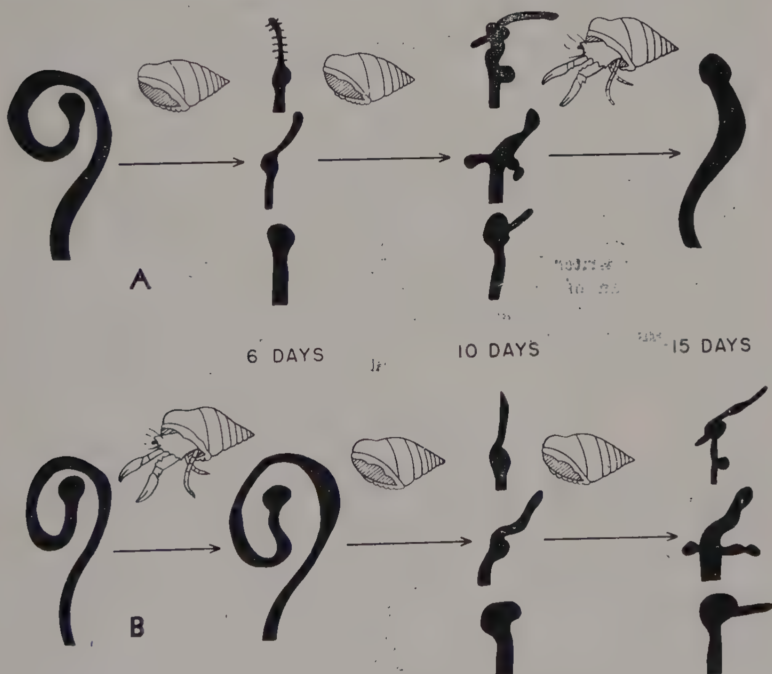

Fig. 2.—Normal and experimental production of spiral zooids. A.—The transformation of spiral zooids on shells from which the crab had been removed. After ten days without the crab, tentacles grow from the end of the hydranth, or else the distal portion of the spiral zooid thins to form a tentacle; medusa buds grow from more proximal portions. Within five days after the crab is returned to the shell small spiral zooids appear. B.—A control experiment run simultaneously with that shown in A. Spiral zooid maintenance continued only so long as the crab was in the shell.

Studies on Virgulate Xiphidiocercariae from Indiana and Michigan[1]

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The Cercariae virgulae was proposed by Lühe (1909) to include five species of xiphidiocercariae containing a pear shaped "organ" in the oral sucker. Since that time, approximately 50 additional species belonging to this group have been described, and in seven instances they have been shown to be larvae of the trematode family Lecithodendriidae. Many of these cercariae have been described so incompletely that if found again their identification would be a matter of conjecture. For that reason a review of the entire group would be of little value here. However, the paper of Seitner (1945) is significant to the present study, as three of the five species of virgulate xiphidiocercariae which he described from Indiana have been studied further by the writer.

Another paper (Hall, 1959) has reported the life history of one of the three; the remaining two are included below with descriptions of ten new virgulate cercariae from Indiana and Michigan.

Acknowledgments.—This study was supported by an XR Fellowship from the Purdue Research Foundation, 1956-1958, and was supervised by Prof. R. M. Cable. The writer is indebted to Dr. F. J. Kruidenier, University of Illinois, for the loan of unpublished notes and drawings of virgulate cercariae, and to Dr. B. E. Montgomery, Purdue University, for aid in identification of insect nymphs and larvae. The writer's associates, L. E. Peters Jr., F. M. Fisher Jr., and T. T. Dunagan aided in the collection of mollusks and arthropods.

Materials and Methods

Prosobranch snails collected and examined for emerging cercariae included 5595 *Pleurocera acuta,* 1831 *Goniobasis livescens,* 467 *Goniobasis* sp., 3953 *Amnicola limosa,* and 680 *Campeloma* sp. Most of the snails were taken from the Wabash and Tippecanoe Rivers near Lafayette, Indiana during the summer and fall of 1956 and 1957, but the unidentified species of *Goniobasis* was obtained from the Pere Marquette River, Michigan, in September, 1956. The various arthropods tested as possible second intermediate hosts were collected from these rivers and from Little Pine Creek near Green Hill, Indiana, where no snails harboring virgulate cercariae could be found. Arthropods were placed with freshly emerged cercariae for 2 to 24 hours, the period of exposure depending on the number of cercariae available.

[1] Based on part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Purdue University, August, 1958.

Cercariae were studied alive and after fixation in hot 3 percent formalin as described elsewhere (Hall, 1959). Measurements are in millimeters and are from specimens fixed in formalin after natural emergence from the snail. Drawings are free hand and to scale from numerous measurements; those of entire, fully developed cercariae are based on formalin fixed material, while those of developing cercariae, sporocysts, and metacercariae are from living material.

OBSERVATIONS

Specific characters of virgulate cercariae include the length and shape of the stylet; size and shape of the virgula organ; position, texture, and staining reactions of the cephalic glands; the arrangement of their ducts; the shape of the excretory bladder; and the flame cell pattern. The following general diagnosis applies to all of the species considered below and is given to avoid repetition of characters which they have in common:

Small distome cercariae, ventral sucker smaller than oral sucker, mouth subterminal. Oral sucker with virgula organ consisting of a pair of sacs containing a homogeneous mucoid substance; sacs fused or not posteriorly and opening within oral sucker near mouth. Stylet set horizontally in oral sucker, with more or less distinct shoulder between the tip and a proximal portion consisting of a sclerotized shaft and a less refractile basal extension of the core. Tail usually attached posteroventrally, but sometimes terminally or posterodorsally, in a more or less distinct depression of the body. Entire body and tail covered with fine spines, often longer or more pronounced on ventral sucker and at tip of tail. Cuticle of body usually with minute papillae, each with a delicate filamentous process. Prepharynx short, pharynx present, esophagus and short ceca sometimes evident. Genital primordium dorsal and posterior to ventral sucker, basically C-shaped, but frequently with lobes representing the developing reproductive organs. Cephalic glands three pairs, more or less in a line on each side of the body, and numbered from anterior to posterior in subsequent descriptions; their ducts in a single bundle or with one duct median to others on each side of forebody. Excretory bladder U- to V-shaped or saccate, its epithelium more evident in some species than in others. Main excretory tubules divide at or posterior to level of ventral sucker to receive an anterior and a posterior collecting tubule, each with three groups of flame cells so that their formula is $2 [(n + n + n) + (n + n + n)]$ with $n = 2$ or 3. Cystogenous glands not obvious, parenchyma usually with refractile spherules resembling oil droplets. Cercariae produced by small spherical to oval sporocysts in the digestive gland of the host and difficult to separate from that tissue.

DESCRIPTION OF SPECIES
(All measurements are in millimeters)

Cercaria tranoglandis Seitner, 1945
(Fig. 1)

Description (Based on larvae from one infected snail).—Body elongate-oval, 0.112-0.132 long, 0.056-0.069 wide, ends rounded in fixed specimens;

at least 9 papillae with setae on each side. Tail 0.081-0.097 long, 0.017-0.019 wide, its attachment postero-ventral; tip with enlarged spines. Oral sucker 0.038-0.049 long, 0.036-0.042 wide; virgula moderately large, 0.037-0.042 long, 0.034-0.038 wide, its right and left halves apparently not fused posteriorly. Stylet 0.020-0.022 long, 0.005 wide at base; tip curved ventrally, tapering gradually from shoulder, then abruptly toward point. Pharynx 0.006-0.010 long, 0.010-0.013 wide; esophagus and intestine not observed. Ventral sucker 0.019 in diameter, its anterior margin 0.073-0.075 from anterior end of body. Genital primordium C-shaped, with irregular margin. Cephalic glands lateral and anterior to ventral sucker with ducts in a single bundle; first pair with coarsest granules, granules of second and third pair finer and nearly equal in size; affinity for neutral red (*intra vitam*) greatest in third pair, less in first, and least in second. A pair of granular bodies at pharyngeal level stain intensely with neutral red. Excretory bladder U- to V-shaped; remainder of excretory system not observed. Sporocysts round to oval, to 0.200 in length.

Host.—*Goniobasis livescens.*

Locality and time of year.—Tippecanoe River, Indiana; August.

Cercaria tranoglandis is distinguished by the coarsely granular, refractile cytoplasm of the first pair of cephalic glands, the finer granules and similar texture of the second and third pair, and the affinity of the third pair for neutral red; the cephalic gland ducts in a single bundle; the granular bodies at the level of the pharynx; the postero-ventral attachment of the tail, and the long spines at its tip.

Emergence of this species was not observed precisely, but it seemed to occur at all hours. Periods of swimming towards the surface alternate with intervals during which the larvae rest and settle slowly in the water. Older ones may creep along the bottom of the container, inchworm fashion.

C. tranoglandis failed to penetrate dragonfly and damselfly naiads (*Ophiogomphus*? sp., *Calopteryx* sp.); mayfly naiads (*Stenonema*? sp.); and alderfly larvae (*Sialis* sp.).

Cercaria tremaglandis n. sp.
(Figs. 2-5)

Specific diagnosis (Based on infections in 4 snails).—Body elongate-oval, 0.118-0.135 long, 0.043-0.064 wide, ends often truncate on fixation; at least 7 papillae with setae on each side. Tail 0.066-0.096 long, 0.013-0.018 wide, attached posteroventrally; tip without enlarged spines. Oral sucker 0.040-0.058 long, 0.035-0.056 wide, with a pair of granular bodies staining deeply with neutral red immediately anterior to virgula organ. Virgula of moderate size, 0.035-0.047 long, 0.030-0.052 wide, its right and left halves not fused posteriorly. Stylet with a length of 0.014-0.019 divided as follows: tip 0.004-0.005, shoulder 0.002-0.003, shaft 0.006-0.008, base 0.0025-0.004; width at shoulder 0.0045-0.006, at base 0.005-0.007. Tip of stylet curved ventrally, tapering gradually from shoulder and then more abruptly toward point (Fig. 3); edges of shaft incurved. Pharynx 0.007-0.012 by 0.010-0.014; esophagus and intestine not observed. Ventral sucker 0.015-0.019 in diameter, with enlarged spines; its anterior margin 0.054-0.073 from anterior end of body. Genital primordium roughly C-shaped with an elongate posterior lobe. Cephalic glands

posterior and lateral to slightly anterior to ventral sucker with ducts in a single bundle; third pair with slightly coarser granules and a slight affinity for neutral red whereas the other pairs are similar in appearance and do not stain with that dye. Excretory bladder U- to V-shaped; main excretory tubules divide posterior to ventral sucker, at level of second or third cephalic gland; flame cell formula 2 [(2 + 2 + 2) + (2 + 2 + 2)]. Sporocyst subspherical, 0.125-0.145 in diameter, containing few embryos.

Host.—Pleurocera acuta.

Localities and time of year.—Wabash and Tippecanoe Rivers, Indiana; June to November.

Cercaria tremaglandis is distinguished by the two granular bodies anterior to the virgula organ, the relative similarity of the cephalic glands in texture and staining reaction, the single bundle of cephalic gland ducts, the abruptly tapering tip of the stylet, and the flame cell pattern.

The cercariae emerged mostly in the late evening and to some extent in the early evening but at no other times. On emergence, their swimming periods are rather prolonged with the larvae not moving in an up and down path as in some of the other species. Instead they swim upwards, usually stop short of the surface, and as they sink through the water, they slowly extend and contract the body and tail. The larvae may resume swimming on or before reaching the bottom of the container, or they may creep over the bottom, especially after they have been shed for some time. No phototactic response was observed.

Cercaria tremaglandis failed to enter dragonfly naiads (*Gomphus* spp., *Hagenius* sp.); caddis fly larvae (*Hydropsyche* sp.); and a small crayfish. It entered and encysted in a stonefly naiad (*Pteronarcys*? sp.) and occasionally mayfly naiads (*Hexagenia limbata*). Seventeen *Hexagenia* naiads from a stream in which virgulate cercariae evidently did not occur were exposed to infection. Of 11 examined 3 hours to 42 days later, five contained metacercariae, probably of *C. tremaglandis*. The longer the interval between exposure and examination, the fewer the metacercariae that were found. The six remaining naiads were held for 14-53 days after which one was fed to each of three newly hatched chicks and the remainder to two hamsters. Examination of these animals three to four days later yielded no trematodes.

Approximately 100 tailless cercariae and recently encysted metacercariae were found in the body cavity of one *Hexagenia* naiad three hours after exposure. The virgula organ and cephalic glands were largely depleted, but the species could be identified by their remnants and by the size and shape of the stylet. The newly formed cysts were spherical and 0.096-0.125 in diameter. Five from a naiad examined 42 days after exposure were spherical (about 0.135 in diameter) to oval (0.162 by 0.096), and had a thick double wall in which was embedded a stylet matching that of *C. tremaglandis*. The body was spiny, and the excretory bladder voluminous, U- to V-shaped, and filled with small concretions not over 0.008 in diameter.

Cercaria notura n. sp.
(Figs. 6-9)

Specific diagnosis (Based on infections in 3 snails).—Body elongate-oval, 0.101-0.158 long, 0.047-0.075 wide, ends usually slightly truncated on fixation; at least one papilla on each side. Tail attached dorsally near posterior end of body, length 0.064-0.097, width 0.013-0.020; with spines longer than on body and somewhat enlarged at tip of tail. Oral sucker 0.035-0.052 long, 0.028-0.051 wide; virgula small to moderate in size, 0.025-0.044 long, 0.027-0.050 wide, its right and left halves not fused posteriorly. Stylet length 0.018-0.019 divided as follows: tip 0.003-0.005, shoulder 0.0025-0.004, shaft 0.009-0.010, base 0.0015-0.0035; width at shoulder 0.0045-0.006, at base 0.004-0.005. Tip of stylet curved ventrally, edges of shaft straight or slightly incurved. Pharynx 0.006-0.008 long, 0.008-0.013 wide; esophagus and intestine not observed. Ventral sucker 0.016-0.022 in diameter; spines around its opening not noticeably enlarged; its anterior margin 0.060-0.087 from anterior end of body. Genital primordium variable, roughly C-shaped to irregularly or regularly lobed. Cephalic glands mostly lateral and posterior to ventral sucker, with ducts in a single bundle; first and third pairs with coarser granules than second pair, granules of first pair being largest. Affinity for neutral red greatest in third pair, less in first and least in second pair. Excretory bladder U- to V-shaped; main excretory tubules divide posterior to ventral sucker; flame cell formula $2 [(3 + 3 + 3) + (3 + 3 + 3)]$. Sporocysts irregular, elongate-oval, or spherical, 0.086-0.264 long, 0.066-0.193 wide; usually with one or sometimes two protuberances and containing two to five developing cercariae.

Host.—*Goniobasis livescens.*

Localities and time of year.—Tippecanoe River, Indiana; June to August.

Cercaria notura is distinguished by the dorsal insertion of the tail, the coarse granules of the first cephalic gland and the intense affinity of the third for neutral red, the single bundle of cephalic gland ducts, and the 18 pairs of flame cells.

There was no apparent periodicity in emergence of the cercariae in the laboratory. They swim towards the surface in a distinctive, jerky, spinning manner and then rest as they settle to the bottom, slowly contracting and extending the body. This species is relatively inactive, and spends much of the time creeping or lying on the bottom, even when recently emerged. In this respect, it resembles *C. nothrica* Seitner but differs from that species in the length of the stylet, tail attachment, and host species. No reaction to light was observed.

Cercaria notura failed to enter various dragonfly and damselfly naiads (*Gomphus* sp., *Dromogomphus* sp., *Ophiogomphus*? sp., *Hetaerina americana*, *Ischnura*? sp., *Argia*? sp.); mayfly naiads (*Stenonema*? sp.); culicine mosquito larvae; and alderfly larvae (*Sialis* sp.).

Cercaria meringura Seitner, 1945
(Figs. 10-12)

Description (Based on infections in 3 snails).—Body relatively large, elongate-oval, 0.157-0.200 long, 0.076-0.114 wide, ends slightly truncate or rounded in heat killed specimens; at least 7 papillae with setae on each side.

Tail attached posteroventrally; 0.099-0.142 long, 0.023-0.030 wide; spinose with spines enlarged at its tip. Oral sucker 0.052-0.073 long, 0.041-0.055 wide; virgula organ conspicuous, 0.027-0.056 long, 0.027-0.053 wide, its right and left halves not fused posteriorly. Stylet length 0.044-0.049 divided as follows: tip 0.010-0.0105, shoulder 0.003-0.004, shaft 0.030-0.033, base 0.002-0.0035; width at shoulder 0.0055-0.007, at base 0.0065-0.008. Tip of stylet curved slightly ventrally, at first tapering gradually from shoulder and then more abruptly toward point; edges of shaft slightly incurved. Pharynx 0.011-0.014 long, 0.0155-0.018 wide; esophagus and intestine not observed. Ventral sucker 0.024-0.028 in diameter, its anterior margin 0.078-0.114 from anterior end of body, opening surrounded by enlarged spines. Genital primordium roughly C-shaped, with one or two rounded posterior lobes. Cephalic glands lateral to ventral sucker and tending to be more posterior than anterior to that sucker; their ducts in a single bundle; all 3 pairs with similar, coarse granules, the third pair only staining with neutral red. Pairs of small, granular bodies near ventral surface from level of pharynx to posterior edge of ventral sucker. Excretory bladder saccate and distinctly epithelial; main excretory tubules divide at level of ventral sucker; flame cell formula $2[(3+3+3)+(3+3+3)]$. Sporocyst up to 0.250 long, containing about 12 cercariae.

Host.—*Goniobasis livescens.*

Locality and time of year.—Tippecanoe River, Indiana; July to November.

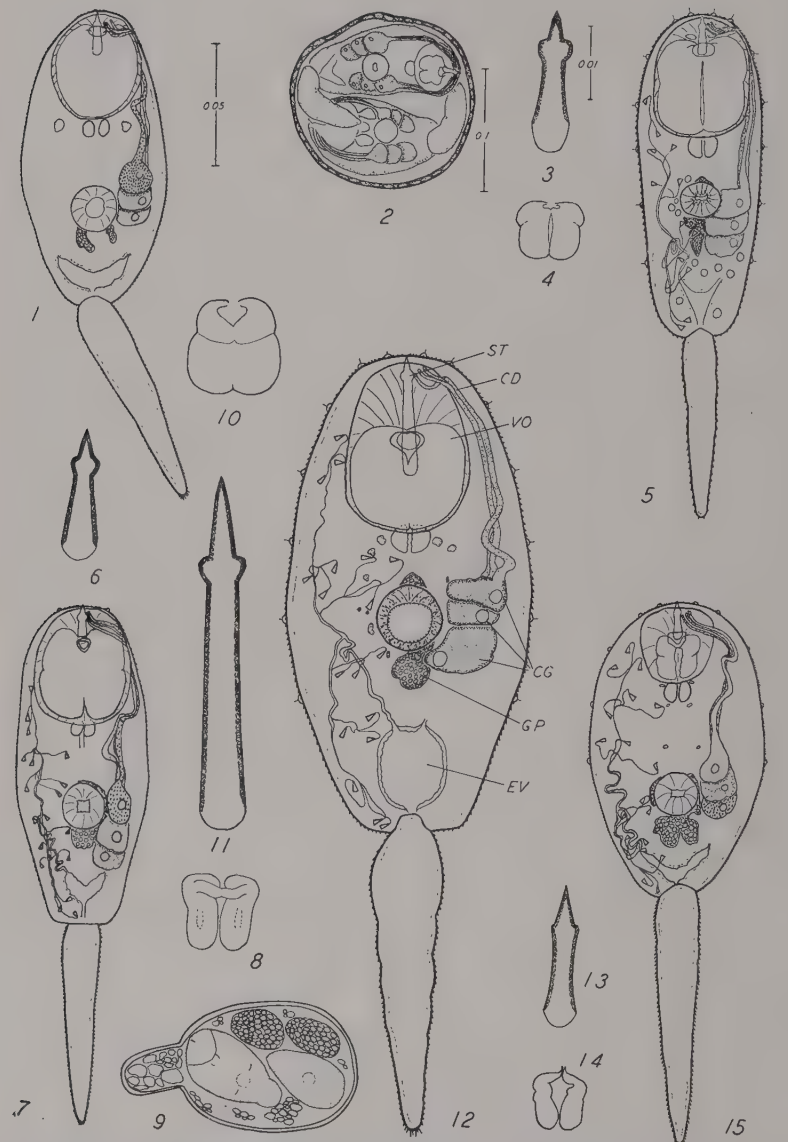
Cercaria meringura is readily distinguished by its large size, the long stylet, the saccate excretory bladder, and the uniformly coarse texture of the cephalic glands.

Some of the snails infected with *C. meringura* were collected in November and held in the laboratory until February for study. At that time, cercariae were shed only in the evening, usually after 9 o'clock. On emergence, they are strong swimmers and stay well above the bottom of the container, but are seldom found near the surface. Swimming periods of at least 1.5 minutes are followed by shorter rest periods during which the larvae sink towards the bottom. As in other species, the older cercariae seldom leave the bottom of the container. No phototactic response was observed.

C. meringura failed to enter dragonfly and damselfly naiads (*Gomphus* sp., *Stylurus spiniceps, Dromogomphus* sp., *Hagenius* sp., *Boyeria* sp., *Macromia* sp., *Calopteryx*? sp., *Ischnura*? sp., *Argia*? sp.); mayfly naiads (*Stenonema*? sp.); alderfly larvae (*Sialis* sp.); and beetle larvae (*Psephenus* sp.).

Cercaria papiliogona n. sp.
(Figs. 13-15)

Specific diagnosis (Based on infections in 7 snails).—Body small, broadly oval, 0.088-0.127 long, 0.053-0.075 wide, ends usually rounded in fixed specimens, rarely truncate; at least 5 papillae on each side. Tail attached posteroventrally, 0.084-0.119 long, 0.013-0.018 wide, with spines longer than on body, somewhat enlarged at tip of tail. Oral sucker 0.027-0.033 long, 0.024-0.032 wide, virgula small, 0.013-0.025 long, 0.015-0.023 wide, its right and left halves not fused posteriorly. Stylet length 0.017-0.021, divided as follows: tip



Figs. 1-15.—All figures except those of virgula organs in living specimens are free hand to scale from numerous measurements of specimens killed in hot 3 percent formalin. Figures of entire cercariae are drawn to the same scale; stylets are represented at 3.0 times, sporocysts and metacercariae at 0.5 times that magnification. 1. *Cercaria tranoglandis,* fully developed specimen, ventral view. 2-5. *Cercaria tremaglandis.* 2. Living sporocyst. 3. Stylet, ventral view.

0.0045-0.006, shoulder 0.002-0.0035, shaft 0.007-0.009, base 0.002-0.003; width at shoulder 0.004-0.005, at base 0.004-0.006. Tip of stylet curved ventrally but straight in dorsal view, shoulder region often indistinct, edges of shaft incurved. Pharynx 0.006-0.012 long, 0.009-0.012 wide; esophagus and intestine not observed. Ventral sucker 0.016-0.019 in diameter, its anterior margin 0.055-0.070 from anterior end of body, spines around opening slightly enlarged. Genital primordium consistently tetralobate, butterfly-shaped. Cephalic glands lateral to ventral sucker and tending to be more anterior than posterior to that sucker; their ducts in a single bundle; third pair with coarsest granules and greatest affinity for neutral red, granules of second pair larger than those of first. Small, paired, granular structures staining with neutral red situated on either side of the pharynx and posterior to that level. Excretory bladder U- to V-shaped; main excretory tubules divide lateral or posterior to ventral sucker; flame cell formula $2\ [(3 + 3 + 3) + (3 + 3 + 3)]$. Sporocysts not studied.

Host.—Pleurocera acuta.

Localities and time of year.—Wabash and Tippecanoe Rivers, Indiana; May to August.

Cercaria papiliogona is distinguished by the shape of the genital primordium and virgula organ which is not fused posteriorly, the coarse texture and deep staining reaction of the third pair of cephalic glands, the indistinct shoulders of the stylet, the flame cell formula, and the shape of the body on fixation.

This species emerged at all hours but in larger numbers during the evening. At first, the swimming movement is prolonged with the cercariae remaining near the bottom, rising and falling slowly and with steady progression. The larvae rest body downward at the bottom of the container with little contracting and extending of the body. As the cercariae age, swimming movements are less prolonged and consist of a jerky, upward spinning; eventually most of the time is spent resting or creeping along the bottom. At room temperature, the cercariae live for 22-40 hours after emergence. There was some evidence of a slight positive response to light.

C. papiliogona failed to enter dragonfly and damselfly naiads (*Gomphus* sp., *Stylurus spiniceps*, *Dromogomphus* sp., *Ophiogomphus*? sp., *Macromia* sp., *Calopteryx* sp., *Hetaerina americana*, *Ischnura*? sp., *Argia*? sp.); mayfly naiads (*Hexagenia limbata*, *Stenonema*? sp.); caddis fly larvae (*Cheumatopsyche*? sp., *Hydropsyche* sp., and

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4. Outline of virgula organ in living specimen, ventral view. 5. Fully developed cercaria, ventral view. 6-9. *Cercaria notura*. 6. Stylet, ventral view. 7. Fully developed cercaria, ventral view. 8. Outline of virgula organ in living specimen, ventral view. 9. Living sporocyst. 10-12. *Cercaria meringura*. 10. Outline of virgula organ in living specimen, ventral view. 11. Stylet, ventral view. 12. Fully developed cercaria, ventral view. 13-15. *Cercaria papiliogona*. 13. Stylet, ventral view. 14. Outline of virgula organ in living specimen, ventral view. 15. Fully developed cercaria, ventral view.

Abbreviations: CD — Cephalic Gland Duct; CG — Cephalic Gland; EV — Excretory Vesicle; GP — Genital Primordium; ST — Stylet; VO — Virgula Organ.

one unidentified species); stonefly naiads (*Perlinella* sp., and one unidentified species); culicine mosquito larvae; chironomid larvae; alderfly larvae (*Sialis* sp.); two unidentified species of beetle larvae; and crayfish.

Cercaria pinguisoma n. sp.
(Figs. 16-19)

Specific diagnosis (Based on infections in 2 snails).—Body broadly oval, 0.114-0.144 long, 0.061-0.078 wide; anterior end usually rounded, posterior end truncate on fixation; cuticular papillae not observed but may be present. Tail attached posteroventrally; length 0.089-0.119, width 0.015-0.020; spines larger than on body, but not pronounced at its tip. Oral sucker 0.046-0.063 long, 0.043-0.053 wide; virgula moderately large, 0.030-0.048 long, 0.036-0.045 wide, its right and left halves not fused posteriorly. Stylet length 0.027-0.029 divided as follows: tip 0.007-0.008, shoulder 0.004-0.0045, shaft 0.011-0.0125, base 0.005-0.006; width at shoulder 0.006-0.0065, at base 0.0075-0.008. Tip of stylet curved ventrally, tapering gradually from shoulder, then more abruptly toward point. Pharynx 0.0075-0.010 long, 0.010-0.013 wide; esophagus and ceca short, the latter not reaching ventral sucker. Ventral sucker 0.017-0.021 in diameter, its anterior margin 0.066-0.073 from anterior end of body; spines around its opening not enlarged. Genital primordium roughly C-shaped with 2 rounded posterior lobes. Cephalic glands lateral to ventral sucker and tending to be more anterior than posterior to that sucker, with ducts in a single convoluted bundle; first pair with the largest granules; granules of third pair larger than those of second pair; all glands except second pair with a pronounced affinity for neutral red. Small, paired granular structures staining with that dye on either side of pharynx, esophagus, and ventral sucker. Excretory bladder U- to V-shaped; main excretory tubules divide at level of posterior border of ventral sucker; flame cell formula $2 [(3 + 3 + 3) + (3 + 3 + 3)]$. Sporocyst subspherical to ovoid, 0.135-0.193 long, 0.107-0.128 wide; containing up to 8 developing cercariae.

Host.—Goniobasis livescens.

Locality and time of year.—Tippecanoe River, Indiana; July to September.

Cercaria pinguisoma is characterized by the broadly oval body shape, relatively large stylet, the moderately large, unfused virgula organ, the texture and staining reaction of the cephalic glands and the arrangement of their ducts, the paired granular masses in the forebody, attachment of the tail, and the flame cell pattern.

This species is usually shed during the early evening hours. On emergence, the cercariae are very active and swim continuously well above the bottom of the container with very occasional rest periods. Progressive inchworm movements are common after the first hour; some hours later the cercariae are found lying motionless on their backs on the bottom of the dish. This species showed a marked tendency to encyst on the slide when mounted for study. Phototropic reactions were not observed.

C. pinguisoma failed to enter dragonfly and damselfly naiads (*Gomphus* sp., *Calopteryx* sp., *Hetaerina americana*); mayfly naiads (*Stenonema*? sp.); beetle larvae (*Psephenus* sp.); and crayfish.

Cercaria bryobulga n. sp.
(Figs. 20-22)

Specific diagnosis (Based on infections in 3 snails).—Body relatively large, elongate-oval, 0.169-0.193 long, 0.056-0.068 wide; usually the anterior end rounded and posterior end truncate on fixation; cuticular papillae not observed but may be present. Tail attached posteroventrally; length 0.079-0.117, width 0.015-0.018; its tip without enlarged spines. Oral sucker 0.058-0.068 long, 0.049-0.062 wide; virgula organ extremely large, 0.054-0.059 long, 0.048-0.058 wide, its right and left halves not fused posteriorly. Stylet length 0.021-0.024, divided as follows: tip 0.005, shoulder 0.003, shaft 0.010, base 0.0045; width at shoulder 0.006, at base 0.007-0.008. Tip of stylet curved ventrally, edges of shaft straight. Pharynx 0.008-0.011 long, 0.013-0.015 wide; esophagus and intestine not observed. Ventral sucker 0.017-0.022 in diameter, its anterior margin 0.086-0.092 from anterior end of body; with enlarged spines around its opening. Genital primordium C-shaped, largely dorsal to ventral sucker. Cephalic glands anterior, lateral, and posterior to ventral sucker, with ducts in a single bundle; third pair with coarse granules, first and second pair similar, with fine granules. Two pairs of small granular bodies staining with neutral red on each side of body immediately anterior to ventral sucker. Excretory bladder small, saccate, distinctly epithelial; main excretory tubules divide lateral to posterior border of ventral sucker; flame cell pattern not determined. Sporocysts not observed.

Host.—*Goniobasis* sp.

Locality and time of year.—Pere Marquette River, Michigan; September.

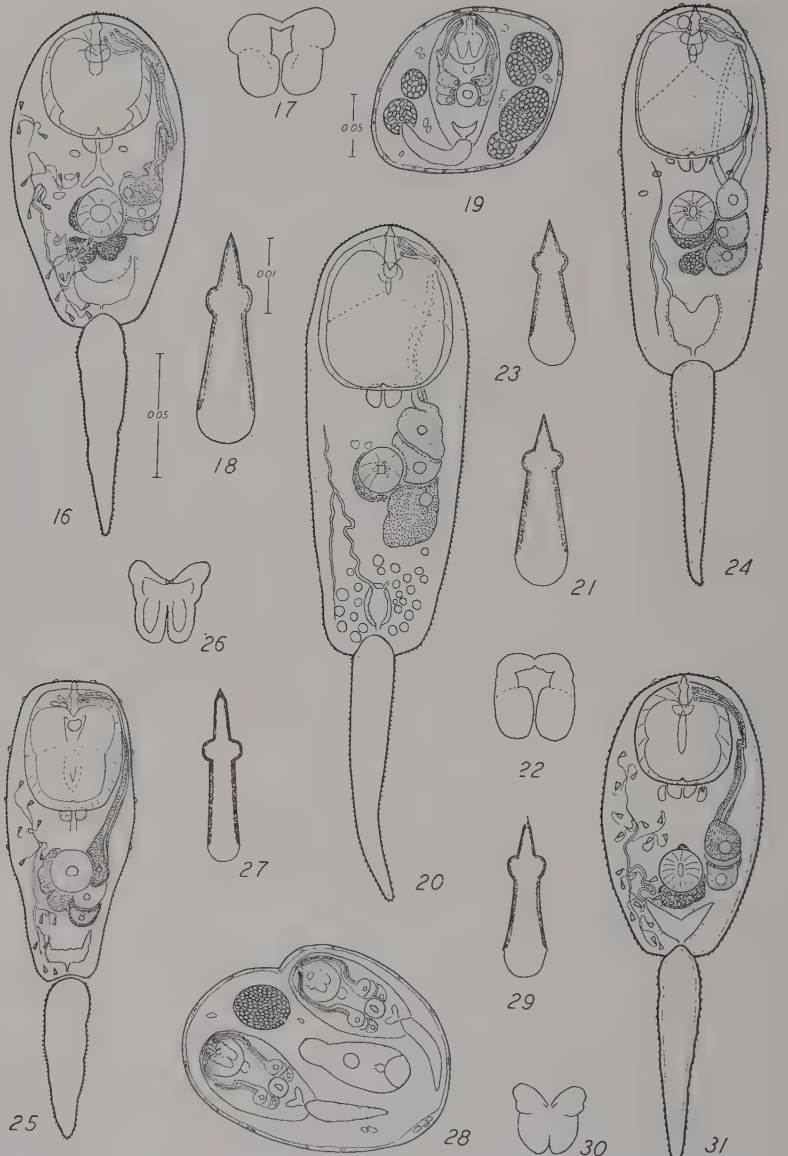
Cercaria bryobulga is characterized by the large, unfused virgula, the size of the body, the texture of the cephalic glands, the granular structures near the ventral sucker, and the shape of the small excretory bladder.

Emergence of this species was not followed closely, but seemed to occur at all hours. The cercariae are strong swimmers and stay well above the bottom of the container. Creeping movements were not observed, nor was any definite reaction to light noted.

C. bryobulga did not enter dragonfly and damselfly naiads (*Dromogomphus* sp., *Hetaerina americana*); and stonefly naiads (two unidentified species).

Cercaria neusticoides n. sp.
(Figs. 23-24)

Specific diagnosis (Based on infection in one snail).—Body elongate-oval, 0.132-0.150 long, 0.050-0.061 wide, ends rounded to slightly truncate on fixation, at least 7 papillae on each side. Tail attached posteroventrally, length 0.083-0.090, width 0.015-0.017; tip without enlarged spines. Oral sucker 0.059-0.063 long, 0.044-0.050 wide, with a pair of refractile spherules, one on each side of stylet at level of shoulder. Virgula large, 0.049-0.055 long, 0.041-0.049 wide, its right and left halves not fused posteriorly. Stylet length 0.018-0.022, divided as follows: tip 0.0035-0.005, shoulder 0.003, shaft 0.008, base 0.004; width at shoulder 0.004-0.005, at base 0.005-0.007. Tip of stylet curved ventrally; edges of shaft nearly straight. Pharynx 0.007-0.009 long, 0.011-0.013 wide; esophagus and intestine not observed. Ventral sucker 0.017-0.020 in diameter, its anterior margin 0.071-0.078 from anterior end of body;



Figs. 16-31.—16-19. *Cercaria pinguisoma.* 16. Fully developed cercaria, ventral view. 17. Outline of virgula organ in living specimen, ventral view. 18. Stylet, ventral view. 19. Living sporocyst. 20-22. *Cercaria bryobulga.* 20. Fully developed cercaria, ventral view. 21. Stylet, ventral view. 22. Outline of virgula organ in living specimen, ventral view. 23-24. *Cercaria neusticoides.* 23. Stylet, ventral view. 24. Fully developed cercaria, ventral view. 25-27.

with enlarged spines around opening. Genital primordium roughly C-shaped. Cephalic glands lateral to ventral sucker and tending to be more posterior than anterior to that sucker; with one duct on each side median to the other 2 in a bundle; texture of all glands nearly equal, the third pair with slightly the coarsest granules and greatest affinity for neutral red. Small, paired, granular structures staining with that dye on either side of body from pharynx to ventral sucker. Excretory bladder U- to V-shaped; main excretory tubules divide just posterior to level of ventral sucker; flame cell pattern not determined. Sporocysts not studied.

Host.—*Pleurocera acuta.*

Locality and time of year.—Tippecanoe River, Indiana; May.

Cercaria neusticoides resembles closely the cercaria of *Mosesia chordeilesia* (syn. *Cercaria neustica* Seitner) in texture and staining reaction of the cephalic glands and in the arrangement of their ducts. It is distinguished from that species by the large, unfused virgula organ, the presence of paired granular structures in the forebody, and the refractile spherules on either side of the stylet.

The time of emergence varies, but there is a tendency for the snail to shed more cercariae in the late afternoon and evening than at other hours. Swimming movements are similar to those of other virgulate species. There seemed to be a slight preference for light areas of the container, but no marked phototropic reaction was observed. The cercariae lived for 22 to 41 hours after emergence.

Cercaria neusticoides failed to enter dragonfly and damselfly naiads (*Gomphus* spp., *Dromogomphus* sp , *Ischnura*? sp., *Argia*? sp.); but penetrated one species of mayfly naiad (*Stenonema*? sp.) without encysting and repeatedly entered and encysted in the body cavity of another species (*Hexagenia limbata*). Actual penetration was not observed, but the cercariae could be seen attaching to various parts of the naiad. The primary cyst is formed within three hours of penetration, measures 0.091-0.121 in diameter, and yields to the movements of the worm; the virgula organ shows varying degrees of depletion but is usually distinct.

Twenty naiads of *Hexagenia limbata* were exposed to *C. neusticoides*. Difficulties were encountered in keeping the insects alive in the laboratory, but there was evidence that the metacercariae did not survive for more than a few days. Thus, *Hexagenia limbata* may not be the natural second intermediate host of *C. neusticoides*.

Cercaria pyxiceps n. sp.
(Figs. 25-27)

Specific diagnosis (Based on an infection in one snail).—Body 0.106-0.120 long, 0.050-0.059 wide, shape characteristic on fixation (Fig. 25) with ends

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Cercaria pyxiceps. 25. Fully developed cercaria, ventral view. 26. Outline of virgula organ in living specimen, ventral view. 27. Stylet, ventral view. 28-31. *Cercaria celatoglandis*. 28. Living sporocyst. 29. Stylet, ventral view. 30. Outline of virgula organ in living specimen, ventral view. 31. Fully developed cercaria, ventral view.

almost always truncate; at least 5 papillae on each side. Tail attached terminally and easily lost, 0.063-0.073 long, 0.014-0.018 wide; with spines larger than on body but not pronounced at tip. Oral sucker 0.045-0.048 long, 0.036-0.044 wide, with 2 pairs of granular bodies staining deeply with neutral red immediately anterior to virgula organ. Virgula of moderate size, 0.033-0.043 long, 0.033-0.038 wide, its right and left halves not fused posteriorly. Stylet length 0.0215-0.023, divided as follows: tip 0.007-0.0075, shoulder 0.002-0.004, shaft 0.008-0.011, base 0.0015-0.0025; width at shoulder 0.0055-0.007, at base 0.004-0.005. Tip of stylet curved ventrally, tapering gradually from shoulder and then more abruptly toward point; edges of shaft almost straight. Pharynx 0.006-0.008 long, 0.011-0.013 wide; posterior part of esophagus and intestine not observed. Ventral sucker 0.017-0.018 in diameter, anterior margin 0.063-0.070 from anterior end of body; without conspicuous spines around opening. Genital primordium roughly C-shaped with rounded posterior lobes. Cephalic glands lateral and posterior to ventral sucker, with ducts in a single bundle; first pair with the coarsest granules, third pair refractile and with coarser granules than second pair; third pair with the greatest affinity for neutral red. Excretory bladder U-shaped; main excretory tubules divide at level of second pair of cephalic glands; flame cell formula $2\ [(2+2+2)\ +\ (2+2+2)]$. Sporocysts not studied.

Host.—*Pleurocera acuta.*

Locality and time of year.—Tippecanoe River, Indiana; June.

Cercaria pyxiceps is characterized by the shape of the body after fixation, the paired granular structures in the oral sucker, the terminal attachment of the tail, the shape of the stylet, and the flame cell formula.

The cercariae usually emerge in the evening and at first swim freely for prolonged periods between which they pause to rest, floating at or near the surface. Later much of the time is spent creeping on the bottom of the container or resting with flexing rather than contracting and extending movements of the body. No distinct reaction to light was observed. *C. pyxiceps* showed a marked tendency to discharge the contents of the first pair of cephalic glands and form a cyst on the slide when living specimens were mounted for study.

Cercaria celatoglandis n. sp.
(Figs. 28-31)

Specific diagnosis (Based on an infection in one snail).—Body broadly oval, 0.103-0.124 long, 0.053-0.064 wide; anterior end usually rounded, posterior end truncate on fixation; at least one papilla on each side. Tail attached posteroventrally, length 0.059-0.085, width 0.015-0.018; tip without enlarged spines. Oral sucker 0.037-0.042 long, 0.034-0.038 wide; virgula small to moderate, 0.030-0.033 long, 0.030-0.036 wide, its right and left halves not fused posteriorly. Stylet length 0.018-0.021, divided as follows: tip 0.004-0.0045, shoulder 0.003-0.0035, shaft 0.0085-0.0095, base 0.0015-0.0045; width at shoulder 0.005-0.0055, at base 0.0055-0.006. Tip of stylet curved ventrally, tapering gradually from shoulder and then more abruptly toward point; edges of shaft incurved. Pharynx 0.0075-0.008 long, 0.0105-0.0125 wide; esophagus and intestine not observed. Ventral sucker 0.0175-0.018 in diameter, its anterior margin 0.064-0.071 from anterior end of body; without enlarged

spines around opening. Genital primordium roughly C-shaped. Cephalic glands anterior and lateral to ventral sucker with ducts in a single bundle; first and third pairs with coarse granules, the latter with the greatest affinity for neutral red; second pair inconspicuous, with fine granules and no affinity for neutral red, often concealed by first pair. A small granular body staining with neutral red on either side of pharynx. Excretory bladder U- to V-shaped, main excretory tubules divide laterally to ventral sucker; flame cell formula 2 [(3 + 3 + 3) + (3 + 3 + 3)]. Sporocysts rounded, oval or irregular; 0.150-0.288 long, 0.121-0.164 wide; containing up to 5 developing cercariae.

Host.—*Goniobasis livescens.*

Locality and time of year.—Tippecanoe River, Indiana; July.

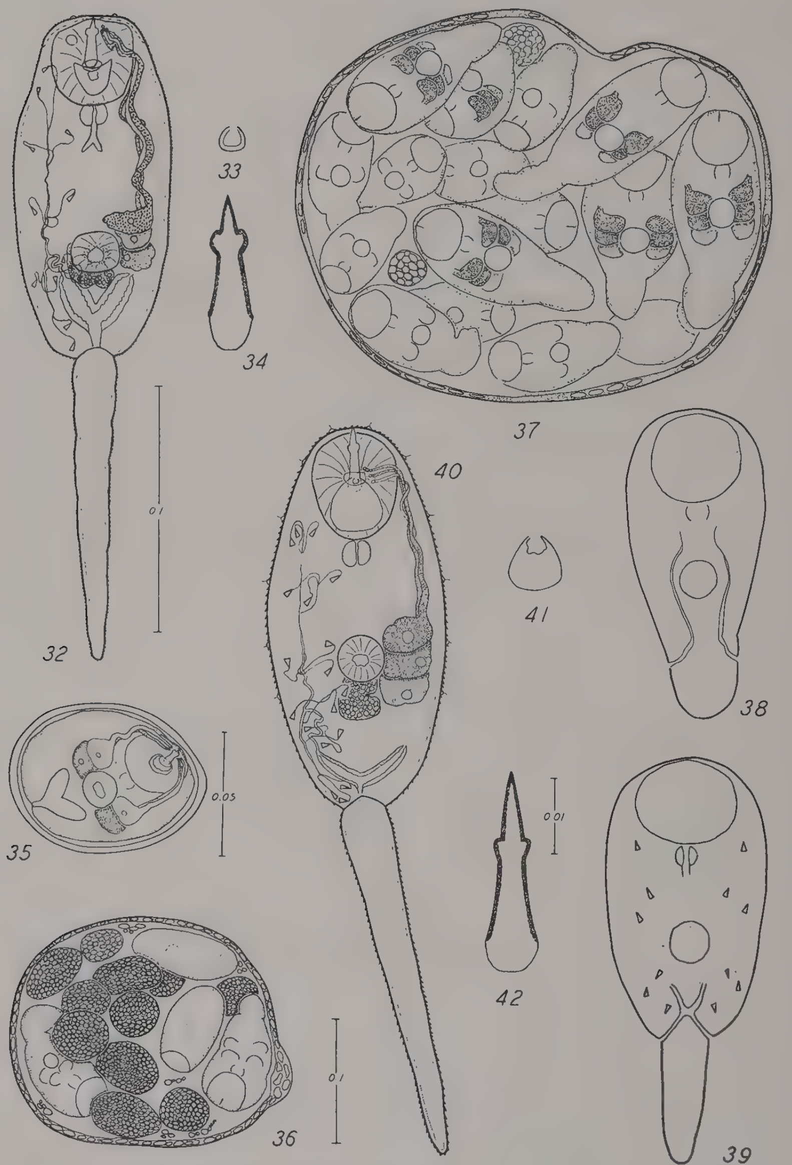
Cercaria celatoglandis is characterized by the coarse texture of the first and third pairs of cephalic glands, the deep staining reaction of the third pair, and the inconspicuous second pair; the granular body on either side of the pharynx; the relatively small stylet; and the excretory pattern.

Emergence is chiefly nocturnal and swimming is at first prolonged. Creeping, and extending and contracting movements of the body are common during rest periods and in older cercariae. There was a tendency towards cyst formation when living specimens were mounted for study, but no encystment occurred in the containers. Phototropic reactions were not observed.

C. celatoglandis did not enter dragonfly and damselfly naiads (*Gomphus* sp., *Hetaerina* sp.) and an unidentified caddis fly larva.

Cercaria adoxovirgula n. sp.
(Figs. 32-36)

Specific diagnosis (Based on infections in 5 snails).—Body elongate-oval; 0.096-0.145 long, 0.048-0.086 wide; ends rounded to truncate, cuticle consistently pulling away from body on fixation; at least one papilla on each side. Tail attached posteroventrally, 0.102-0.146 long, 0.013-0.020 wide; its tip without enlarged spines. Oral sucker 0.026-0.039 long, 0.027-0.037 wide, with refractile spherule on each side of stylet at level of shoulder. Virgula extremely small; 0.008-0.020 long, 0.011-0.024 wide; appearing as an obscure, refractile ring surrounding the oral cavity in living specimens; its right and left halves fused posteriorly. Stylet 0.019-0.022 long, tip 0.0045-0.006, shoulder 0.002-0.004, shaft 0.0075-0.0095, base 0.0035-0.0055; width at shoulder 0.004-0.006, at base 0.0045-0.007. Tip of stylet curved ventrally, its lateral edges curving toward point; edges of shaft straight or slightly incurved. Pharynx 0.007-0.010 long, 0.009-0.0115 wide; esophagus and ceca short, the latter terminating about 1/3 of the body length from anterior end. Ventral sucker 0.018-0.022 in diameter, its anterior margin 0.052-0.091 from anterior end of body; its opening surrounded by enlarged spines. Genital primordium roughly C-shaped to tetralobate. Cephalic glands lateral and anterior to ventral sucker, with ducts in a single bundle; first pair with the largest granules, granules of third pair larger than those of second; third pair with the greatest affinity for neutral red, first pair staining more than second pair. Excretory bladder U- to V-shaped, its epithelial nature evident; main excretory tubules divide lateral or posterior to ventral sucker; flame cell formula 2 [(2 + 2 + 2) +



Figs. 32-42.—32-36. *Cercaria adoxovirgula.* 32. Fully developed cercaria, ventral view. 33. Outline of virgula organ in living specimen, ventral view. 34. Stylet, ventral view. 35. Living metacercaria from body cavity of caddis fly larva 8 hours after exposure to cercariae. 36. Living sporocyst. 37-42. *Cercaria cordivirgula.* 37. Living sporocyst. 38. Developing cercaria showing open-

(2 + 2 + 2)]. Sporocysts round to oval, 0.218 long, 0.185 wide, containing up to 15 developing cercariae.

Host.—*Pleurocera acuta.*

Localities and time of year.—Wabash and Tippecanoe Rivers, Indiana; August and September.

Cercaria adoxovirgula is distinguished by the small, fused, virgula organ; the coarse granules of the first pair of cephalic glands, and the intense affinity of the third pair for neutral red; the pair of refractile spherules in the oral sucker; and the flame cell pattern.

Emergence of this species is almost entirely at night. Natatory movements are similar to those of other virgulate species except that the body is usually more extended and swimming periods are considerably shorter, usually no longer than 30 seconds, and always less than three minutes. The cercariae usually swim upwards, stopping at or near the surface. Several hours after emergence, they rarely leave the bottom of the container where they lie motionless or slowly contract and extend the body. There was some tendency to form a cyst when mounted for study, but no encystment occurred in the containers. There were no definite reactions to light.

C. adoxovirgula failed to penetrate various dragonfly and damselfly naiads (*Gomphus* sp., *Dromogomphus* sp., *Ophiogomphus*? sp., *Calopteryx* sp., *Hetaerina americana, Ischnura*? sp.); mayfly naiads (*Hexagenia limbata, Stenonema*? sp.); stonefly naiads (*Perlinella*? sp. and one unidentified species); and crayfish. Large numbers entered but did not encyst in an alderfly larva (*Sialis* sp.) on one occasion, but later attempts to repeat the experiment were unsuccessful. On several occasions, penetration and encystment were observed in various chironomid larvae, but work with those insects was hindered by difficulties in keeping them alive in the laboratory.

Penetration and encystment also occurred repeatedly on exposure of caddis fly larvae (*Hydropsyche* sp.) from a stream in which virgulate cercariae were not found. Formation of the cyst occurs within seven hours after penetration (Fig. 35). It is oval, 0.073-0.092 long, 0.053-0.068 wide; the primary cyst wall is thin and hyaline with a pinkish cast. The first pair of cephalic glands is depleted, and the virgula organ has lost some of its contents but is still recognizable.

Fifty hydropsychid larvae were exposed to *C. adoxovirgula* and placed in aerated water in battery jars with stones and gravel from the natural habitat of the larvae, but they could not be kept alive longer than four to six weeks. Examination of dead or dying larvae indicated that the metacercariae did not survive longer than three days. It thus seems that the hydropsychid species used is not the natural second intermediate host of *C. adoxovirgula*.

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ings of primary excretory tubules. 39. Later stages of developing cercaria showing fusion of primary excretory tubules. 40. Fully developed cercaria, ventral view. 41. Outline of virgula organ in living specimen, ventral view. 42. Stylet, ventral view.

Cercaria cordivirgula n. sp.
(Figs. 37-42)

Specific diagnosis (Based on infections in 2 snails).—Body elongate-oval, 0.147-0.162 long, 0.066-0.079 wide, ends usually rounded on fixation; at least 6 papillae with setae on each side. Tail attached posteroventrally, 0.139-0.157 long, 0.018-0.0215 wide; its tip without enlarged spines. Oral sucker 0.041-0.044 long, 0.033-0.035 wide; virgula small, cordiform, 0.021-0.023 long, 0.022-0.025 wide, its right and left halves fused posteriorly in emerged cercariae. Stylet length 0.025-0.027, divided as follows: tip 0.008-0.009, shoulder 0.002-0.0035, shaft 0.010-0.012, base 0.0035-0.0045; width at shoulder 0.0045-0.0055, at base 0.006-0.0075. Edges of stylet shaft incurved. Pharynx 0.010-0.011 long, 0.011-0.012 wide; esophagus and intestine not observed. Ventral sucker 0.019-0.020 in diameter, anterior margin 0.078-0.086 from anterior end of body; without enlarged spines around opening. Genital primordium roughly C-shaped. Cephalic glands anterior, lateral, and posterior to ventral sucker, with ducts in a single bundle; first and second pairs with coarse granules and little or no affinity for neutral red; third pair refractile, finely granular, and staining with that dye. Excretory bladder U- to crescent-shaped, its epithelium pronounced; main excretory tubules divide posterior to ventral sucker; flame cell formula $2\ [(3 + 3 + 3) + (3 + 3 + 3)]$. Sporocysts round, oval, or irregular, 0.207-0.434 long, 0.171-0.356 wide, containing 6-21 developing cercariae.

Host.—*Pleurocera acuta.*

Locality and time of year.—Wabash River, Indiana; November.

Cercaria cordivirgula is distinguished by the small, fused, heart-shaped virgula organ, the shape of the stylet, the texture and staining reaction of the cephalic glands, and the flame cell pattern.

A few observations were made on developing cercariae, in some of which were seen the pair of mucoid-containing sacs which eventually fuse in the oral sucker to give rise to the virgula organ of the completely developed larva. In the youngest embryos in which features of the excretory system were observed (Fig. 38), the primary excretory pores were seen at the body-tail furrow and the primary tubules had not united. In more advanced embryos (Fig. 39), the tubules had fused to form the bladder and six flame cells were seen on each side of the body. Their capillaries and the primordium of the excretory epithelium were not observed.

Cercaria cordivirgula emerges mostly at night. Definite reactions to light were not evident. This species did not enter dragonfly and damselfly naiads (*Gomphus* sp., *Calopteryx* sp.); mayfly naiads (*Hexagenia limbata, Isonychia*? sp.); and caddis fly larvae (*Hydropsyche* sp.). Penetration of a stonefly naiad, *Isoperla* sp., by a limited number of cercariae was observed; encystment did not occur within 20 hours, however, and the experiment was not repeated.

DISCUSSION

In addition to the ten new species of virgulate cercariae described above, nine others have been reported from the United States. They

include the five species described by Seitner (1945), *Cercaria geddesi* Ameel 1939, the cercaria of *Cephalophallus obscurus* Macy and Moore 1954, and the cercariae of *Allassogonoporus vespertilionis* and *Acanthatrium oregonense* reported by Knight and Pratt (1955). Faust (1921) described two species of xiphidiocercariae from *Goniobasis carinifera* in Georgia. According to his description and figures, they may well be of the virgulate type and, for that reason, are included in the key below. One species, *Cercaria camilla,* is described as having "an enormous prepharyngeal pocket . . . with a thick semi-muscular, semi-mucoid wall." In the other, *Cercaria tabitha,* "the large oral sucker . . . is provided internally with a thick mucoid substance resembling that of the stylet."

KEY TO VIRGULATE XIPHIDIOCERCARIAE OF NORTH AMERICA
(All measurements of the virgula organ taken from specimens killed in hot 3 percent formalin)

1. With 2 pairs of cephalic glands. Stylet 0.014 long. .... Cercaria of *Acanthatrium oregonense.*
   With 3 pairs of cephalic glands. 4
   With 4 pairs of cephalic glands. 2
2. Ducts of cephalic glands pass anteriorly in a single bundle. 3
   Ducts of one pair of cephalic glands median to those of others. .... *Cercaria geddesi.*
3. Stylet blunt, with distinct shoulder region; sporocysts in *Goniobasis carinifera.* .... *Cercaria tabitha.*
   Stylet sharp, without distinct shoulder, 0.024-0.027 long; sporocysts in *Fluminicola virens.* .... Cercaria of *Cephalophallus obscurus.*
4. Virgula organ within oral sucker. 5
   Large virgula organ posterior (?) to oral sucker; sporocysts in *Goniobasis carinifera.* .... *Cercaria camilla.*
5. Excretory bladder saccate, its epithelium distinct. 6
   Excretory bladder U-, V-, Y-, or crescent-shaped, its epithelial lining usually not distinct. 8
6. Stylet 0.044-0.049 long. .... *Cercaria meringura.*
   Stylet not over 0.025. 7
7. Stylet 0.016 long; sporocysts in *Fluminicola virens.* .... Cercaria of *Allassogonoporus vespertilionis.*
   Stylet 0.020-0.024 long, third pair of cephalic glands with coarser granules than others; sporocysts in *Goniobasis* sp. .... *Cercaria bryobulga.*
8. Cephalic gland ducts extend anteriad in a single bundle. 10
   One pair of cephalic gland ducts median to others. 9
9. Virgula organ small, 0.019-0.027 long, fused posteriorly; no paired granular structures staining with neutral red near pharynx and ventral sucker. .... Cercaria of *Mosesia chordeilesia.*
   Virgula organ large, 0.049-0.055, not fused posteriorly; granular structures present. .... *Cercaria neusticoides.*
10. Stylet shorter than 0.024. 12
    Stylet longer than 0.024. 11
11. Stylet 0.025-0.027 long. Virgula organ small, 0.020-0.023 long, fused posteriorly. .... *Cercaria cordivirgula.*

Stylet 0.027-0.029 long. Virgula organ 0.030-0.048 long, not fused posteriorly. .... *Cercaria pinguisoma.*

12. Oral sucker with paired granular structures staining with neutral red anterior to virgula organ. 13
Oral sucker without such structures. 14

13. Two pairs of granular structures anterior to virgula organ. Stylet tip at least 0.007 long. Granules of first pair of cephalic glands decidedly coarser than in second pair. .... *Cercaria pyxiceps.*
One pair of granular structures anterior to virgula organ. Stylet tip never longer than 0.005. Texture of first and second pairs of cephalic glands equal. .... *Cercaria tremaglandis.*

14. First 2 pairs of cephalic glands of equal or nearly equal texture, granules of third pair distinctly coarser than others. .... *Cercaria nyxetica.*
First 2 pairs of cephalic glands not similar in texture. 15

15. Second and third pairs of cephalic glands of equal or nearly equal texture. 16
Second and third pairs of cephalic glands of very different texture. 17

16. Anterior pair of cephalic glands exceedingly prominent, with very coarse granules. A pair of granular bodies at level of pharynx staining well with neutral red. .... *Cercaria tranoglandis.*
Anterior pair of cephalic glands not prominent. No granular bodies near pharynx. .... *Cercaria nothrica.*

17. Tail attachment posterodorsal. .... *Cercaria notura.*
Tail attachment posteroventral. 18

18. Virgula organ fused posteriorly, indistinct, 0.008-0.020 long. Flame cell formula $2 [(2 + 2 + 2) + (2 + 2 + 2)]$. .... *Cercaria adoxovirgula.*
Virgula organ distinct, not fused posteriorly; flame cell formula $2 [(3 + 3 + 3) + (3 + 3 + 3)]$. 19

19. Genital primordium C-shaped. Virgula organ 0.030-0.033 long; granules of first and third pairs of cephalic glands coarse, those of second pair very fine. .... *Cercaria celatoglandis.*
Genital primordium tetralobate. Virgula organ 0.013-0.025 long; third pair of cephalic glands with coarsest granules, those of second pair coarser than in first pair. .... *Cercaria papiliogona.*

SUMMARY

Twelve virgulate xiphidiocercariae are reported, ten as new species. They are *Cercaria tremaglandis* n. sp., *C. papiliogona* n. sp., *C. adoxovirgula* n. sp., *C. neusticoides* n. sp., *C. pyxiceps* n. sp., and *C. cordivirgula* n. sp., all from *Pleurocera acuta; Cercaria bryobulga* n. sp. from *Goniobasis* sp.; and *Cercaria notura* n. sp., *C. pinguisoma* n. sp., and *C. celatoglandis* n. sp. from *Goniobasis livescens.* The remaining two are *C. tranoglandis* Seitner and *C. meringura* Seitner which are redescribed.

The excretory pattern was determined for nine species and found to be either $2 [(2 + 2 + 2) + (2 + 2 + 2)]$ or $2 [(3 + 3 + 3) + (3 + 3 + 3)]$. Observations on potential second intermediate hosts are recorded, and a key to the virgulate xiphidiocercariae of North America is included.

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Notes and Discussion

Additions to the Flora of Kalamazoo County, Michigan[1]

Since the establishment of Michigan State University's Kellogg Gull Lake Biological Station in 1954, Hanes' (*Flora of Kalamazoo County, Michigan: Vascular Plants,* The Anthoensen Press, Portland, Maine, 295 pp., 1947) Flora has become the basic reference for both the presence of species in the county and geographical location for unusual plants to be used in class demonstration. During the years that the Biological Station has been in operation, seventeen species not listed by the Hanes have been collected in the county.

Seven of these additional species are ruderal elements (see Dansereau, *Biogeography: An Ecological Perspective,* p. 43, 1957); three have escaped from cultivation; and one is a form of a species listed by the Hanes. Others are elements in old-field succession or ground-cover in wooded areas.

The list of additional species, with collection locations, habitat notes, and abundance data, follows. The nomenclature is that of Fernald (*Gray's Manual of Botany,* 8th ed., 1632 pp., 1950).

PINACEAE

Juniperus horizontalis Moench. Creeping Juniper.—Infrequent. Old-field succession. North-east quarter of the south-east quarter, section 21, Ross Township. (T1S:R9W).

LILIACEAE

Polygonatum canaliculatum (Muhl.) Pursh. Channelled Solomon's Seal.—Infrequent member of herbaceous ground cover in Maple-Basswood woodlot. Kellogg Forest. (T1S:R9W; Sec. 22. Ross Township).

JUGLANDACEAE

Carya tomentosa Nutt. Mockernut Hickory.—Frequent canopy tree of Oak-Hickory woodlot, north-west quarter of south-east quarter, section 6, Ross Township.

RANUNCULACEAE

Thalictrum polygamum Muhl. Tall Meadow-Rue. — Frequent. Wet-meadow along Agusta Creek, Section 22, Ross Township. (T1S:R9W).

CRUCIFERAE

Diplotaxis tenuifolia (L.) D. C. Wall Rocket.—Frequent ruderal element on parking-lot fill, trailer area, Biological Station. (T1S:R9W; Sec. 6. Ross Township).

ROSACEAE

Rosa nitida Willd. Shining Rose.—Uncommon. Along bank of Agusta Creek north from Headquarters house, Kellogg Forest. (T1S:R9W; Sec. 22. Ross Township).

LEGUMINOSAE

Lotus corniculatus L. Birdsfoot-Trefoil.—Frequent along roadside banks and in mixed hay fields on Kellogg Farm. (T1S:R9W; Sec. 5, 6, 8. Ross Township).

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[1] Contribution No. 59-19 from the Department of Botany and Plant Pathology, Michigan State University. This work was supported in part by a grant from All-University Research Funds.

EUPHORBIACEAE

Euphorbia humistrata Engelm. Hairy Spreading Spurge.—Common ruderal in cracks and along edges of concrete walks of main campus, Biological Station. (T1S:R9W; Sec. Ross Township).

ANACARDIACEAE

Rhus aromatica Ait. Fragrant Sumac. Uncommon. High ground above west bank of Wintergreen Lake. North-east quarter of south-east quarter, section 8, Ross Township. (T1S:R9W).

Rhus glabra L. *forma laciniata* (Carr.) Robins.—Infrequent. Border of Oak-Hickory woodlot, north-west quarter of south-east quarter, section 6, Ross Township. (T1S:R9W).

CELASTRACEAE

Euonymus europaeus L. European Spindle Tree.—Infrequent. Escape in natural shrub border, top of roadcut, north of main campus, Biological Station. (T1S:R9W; Section 6. Ross Township).

LYTHRACEAE

Lythrum salicaria L. Spiked Loosestrife.—Common. South-west shore of Mud (Stony) Lake, section 22, and along low, wet, banks of Agusta Creek, south-east quarter of north-east quarter, section 21, Ross Township. (T1S:-R9W). Taylor (*The Guide to Garden Flowers,* 131 pp., 1958) considers natural stands of this species to have escaped from cultivation.

LABIATAE

Galeopsis Tetrahit L. Hemp-Nettle.—Infrequent ruderal element of flower-beds, main campus, Biological Station. (T1S:R9W; Sec. 6. Ross Township).

Hyssopus officinalis L. Hyssop.—Infrequent member of old field succession, high ground above west shore of Wintergreen Lake, north-east quarter of the south-east quarter, section 8, Ross Township. (T1S:R9W).

SCROPHULARIACEAE

Veronica chamaedrys L. Birds-eye Speedwell.—Frequent ruderal element in lawns of main campus, Biological Station. (T1S:R9W; Sec. 6, Ross Township).

CAPRIFOLIACEAE

Viburnum denatum L. Southern Arrow-wood.—Common member of natural shrub border on road-cut, north of main campus, Biological Station. An escape. (T1S:R9W; Section 6. Ross Township).

COMPOSITAE

Hieracium paniculatum L. Panicled Hawkweed.—Infrequent ruderal element in flower-beds, main campus, Biological Station. (T1S:R9W; Sec. 6. Ross Township).—JACK C. ELLIOTT, Michigan State University, East Lansing (Present address: Professor of Biology [Botany]. University of Wyoming Team, Faculty of Agriculture, University of Kabul. Kabul, Afghanistan).

A Note to Rotifer Investigators

Announcement is made of the availability of the *Second Preliminary List of the World's Rotifer Students.* This list contains the latest addresses of rotifer workers. The chore of finding addresses for correspondence, exchange of data and reprints is ended. The list is free to workers in this field. Write to: Dr. John J. Gallagher, 1716 E. Terry, Pocatello, Idaho.

A Note Refuting the Suggestion That Some Crayfishes of Northern States Spawn in Winter

There is a seemingly widespread belief that the crayfish *Cambarus b. bartoni,* and also crayfishes of some other species as well, spawn throughout the winter. This belief probably stems from the 1906 paper of Arnold E. Ortmann (*Mem. Carnegie Mus.,* **2**:343-533). Collecting in Pennsylvania, Ortmann found ovigerous *bartoni* females in July and August, and females bearing young in March, August, September and November. In February of 1898, at Princeton, N.J. (the date was not recorded, but was given as towards the end of the month), Ortmann also found a *bartoni* female carrying young. To the writer's knowledge, Ortmann's report of a northern crayfish found with young in winter, is singular, not only for *C. b. bartoni,* but for all northern crayfish.

Ortmann then suggested that the young found in February must have been in the egg stage in January, and that the lack of a December report was probably due to the incompleteness of investigations. Thus he accounted for all the winter months and suggested that *C. b. bartoni* and other "cool water" types may be expected to spawn throughout the year.

Unfortunately, Ortmann gave no details about his winter find, save the general area (Princeton, N. J.), and roughly, the time of the month. He did, however, state that there were only ten young, and he suggests that other young may have escaped. This also suggests, however, that these young were probably well advanced in their development.

On February 27, 1959, the writer found a *C. b. bartoni* female with young in Catatonk Creek, a few miles north of Candor, Tioga county, New York. This creek is a good collecting place for *C. b. bartoni.* The creek was covered with ice from bank to bank in places, but the collecting area was extensively open, with but a bit of ice along the banks. The water temperature was 5.5°C., and the water flow was moderate. The female with young was the eleventh crayfish collected that day. All were very immobile, made no active movements, and were simply picked up from the bottom by hand, after turning the stones that sheltered them.

The female and young were immediately taken to the laboratory and there placed in a tank of water at room temperature (19°C.) after allowing for a gradual warming. In the warm tank water, the female was immediately quite active, and thereby dislodged all of the young, numbering 41. The young were scattered about the two-gallon tank, and 16 hours later were still scattered, none being attached to the female which remained under a rock shelter.

Four young were removed and preserved. They were heavily pigmented, very hairy, and very "dirty" in appearance as is indicative of crayfishes that have not recently molted. They ranged in size from 5.2 to 5.5 mm carapace length, had a five-membered tail fan, and in three young, the first pleopods were just in evidence as buds. In addition, all four young had numerous growths on their exoskeletons of a colonial ciliate, probably *Epistylis cambari.* These growths may also be indicative of crayfish immobility and of a recent lack of molting.

Considering the inactive state of all of the 11 crayfish collected at this time, and the size, stage of development, and general appearance of the young, it is difficult to believe that these young were spawned sometime during the winter, and then underwent a number of molts. It would seem that the possibility must be considered that these young were oviposited in the fall, and had

hatched but were still with the female parent when cold water temperatures immobilized the female and her attached young, and thereby arrested the development of the young. Ortmann did not consider this possibility in his paper, but it is here suggested that the young he found in February were also spawned in the fall, and not in January as Ortmann suggested. If any northern crayfish do oviposit, hatch and rear young through the winter, it remains to be substantiated.—LAWRENCE R. MCMANUS, Cornell University, Ithaca, New York.

The Pronghorn, Antilocapra americana, in Western Iowa

Nelson (Bull. U. S. Dept. Agric., 1346:2, fig. 1, 1925) and Hall and Kelson (The mammals of North America, p. 1023, fig. 495, 1959) mapped the former distribution of the pronghorn, *Antilocapra americana,* as extending eastward to extreme western Iowa. The occurrence of the species in that state has, however, never been documented in the scientific literature; nevertheless, there is an historical record of the pronghorn in western Iowa.

In the spring of 1850 T. A. Culbertson left St. Joseph, Missouri, by horseback with a small group of companions and traveled along the Iowa side of the Missouri River, headed for the badlands of South Dakota and the Upper Missouri region (see Culbertson's account, "Journal of an expedition to the Mauvaises Terres and the Upper Missouri in 1850" edited by J. F. McDermott, Bull. Bureau Amer. Ethnol., 147:viii + 1-164, 1952). The party traveled mostly on the "rolling prairie" just east of the Missouri River. On April 7, 1850, in what is now western Harrison County, Iowa, Culbertson wrote (p. 30): "To-day we passed Willow Creek, two forks of the Soldier River, and the main branch itself, and are now on the bank of the Little Sioux [River] ready to cross it in the morning. Had some elk meat for dinner to-day *and the men saw four antelopes* [italics mine]." On the following day the party crossed the Little Sioux, which took until noon, and during the course of the afternoon in northwestern Harrison County or southwestern Monona County saw (p. 31) "*. . . several antelopes in full flight . . . along the prairie* [italics mine]." The areas in Harrison and Monona counties where pronghorns were seen are between 41° 30′ and 42° 00′ north latitude, and are opposite Burt and Washington counties, Nebraska.

Probably the Missouri River, or more precisely its deciduous riparian association, served as a barrier to the distribution of pronghorns at the latitude of Iowa and Nebraska. Farther to the north in southern and central South Dakota, however, the deciduous association along the river became narrower, and even discontinuous in some places. Here no barrier to the dispersal of pronghorns existed and the species ranged eastward to southwestern Minnesota (Hall and Kelson, *op. cit.*:1022) and southward on the eastern side of the Missouri into western Iowa. Other reports of occurrence of pronghorns in western Iowa probably are in the historical literature dealing with that area. —J. KNOX JONES, JR., Museum of Natural History, University of Kansas, Lawrence.

Book Reviews

Geology of the Great Lakes. By Jack L. Hough. The University of Illinois Press, Urbana, Illinois. 313 pp., 75 figs. including 26 lake stage maps, 22 tables. 1958. $8.50.

This book gives a comprehensive account of the origin and history of the five Great Lakes of North America. Dr. Hough was selected as the recipient of the Kirk Bryan Memorial Award presented by the Geological Society of America for this work "which represents a modern interpretation of the late Pleistocene and post-glacial history of the lakes." Geologically speaking, lakes such as the Great Lakes are ephemeral. They came into existence some 15,000 to 20,000 or more years ago with the wane and retreat of the last continental ice sheet. Resting on a truncated bedrock surface which ranges from Precambrian to Carboniferous rocks, the Great Lakes developed between land and ice with increments of differential erosion and deposition through the energy of water — streams, waves, currents, and other periodic fluctuations. It is this recent geological history gathered from a fragmentary record which is complex and difficult to decipher in the detail that is indicated in the book.

In 1915 the United States Geological Survey published Monograph 53, Leverett and Taylor's classic "The Pleistocene of Indiana and Michigan and the History of the Great Lakes." During the intervening 43 years, much research has been and is being done on the geology of the Great Lakes so that Hough's full treatment is most welcome. Hough started research on this subject in 1932. The bibliography lists 7 publications on Great Lakes geology which he has contributed.

The book is written in two parts. The first part discusses the Great Lakes region, present lakes and pre-lake history, and methods of dating events of lake history. Much factual physical data is given concerning areal size of lakes, depths of water, bottom topography, geological setting, dynamics and chemistry of lake water, a brief discussion of lake sediments and a condensed account of pre-glacial and glacial history of the lakes with an introduction to methods of dating such chronology. Laymen and scientists working in related fields will find much information and handy reference in this portion of the book.

The second part deals with a well-documented interpretation of the detailed chronology of lakes development. The history of the individual lakes is correlated and integrated into the history of the entire Lakes. This part of the book discusses drainage directions, outlets, and changes, high and low water stages, beach development and hinge-line changes due to isostasy.

The author has summarized in chart form (table 22) the correlation of events of Great Lakes history with absolute chronology based upon radiocarbon dates. He has made this more graphic and understandable by including 26 lake stage development maps which take them from the time the basins were occupied by continental glacial ice through their high and low stages to the present modern Great Lakes. The book concludes with an excellent bibliography of 231 references which gives the reader basic sources for much of the information used.

Hough's interpretations based upon sound principle are forthright and admittedly tentative. Printing costs undoubtedly limited the book's content but several omissions are noted. It needs the perspective of a large scale map covering the entire area of the lakes. Information given for single lakes such as the bottom topographic configuration and current directions could have been compiled on the larger map along with the bedrock geology including specula-

tive projection of the formations under the lakes, hinge lines, dunes areas, etc. Other things not included cover information and references to dunes areas some of which are classic, discussion related to the engineering aspects of the lakes, more on the biology and sediments of the lakes, rates of ice retreat, and inclusion of authors in the index for reference checks.

The book is directed primarily to the geologist but since the lakes are used for water supply, navigation and transportation, food supply, recreation, and are involved in various conservation and engineering projects, other people will find the information useful. Biologists, particularly limnologists, ecologists, and conservationists, along with engineers, will find much basic data and history closely related to their interests.

The symposium on the Great Lakes conducted by the Geology and Geography section of the American Association for the Advancement of Science at the annual meeting in Chicago, December 28-29, 1959, is a recent sequel to Hough's book.—RAYMOND C. GUTSCHICK, Department of Geology, University of Notre Dame, Notre Dame, Indiana.

POISONOUS AMPHIBIANS AND REPTILES RECOGNITION AND BITE TREATMENT. By Floyd Boys and Hobart M. Smith. C. C. Thomas, Springfield, Illinois. 149 pp. 1959. $4.75.

The authors treat a very difficult and admittedly confusing problem in an interesting though sometimes prolix manner. The subject matter is divided into nine parts. Included are sections on the taxonomy of venomous animals, the chemistry and mode of action of the poisons of certain amphibians and reptiles, and the first aid and medical treatment for the injuries inflicted by these animals. The sections on the general zoological characteristics of venomous reptiles, general precautions against snakebite, and the recognition and distribution of venomous animals are accurate and adequate. The drawings, pictures and maps are well done. The various sections dealing with the chemistry, mode of action of the poison and treatment of the envenomated victim are somewhat of a *mare liberum* and will raise a number of Hippocratic eyebrows.

Snake venoms are complex mixtures, chiefly proteins, many of which have enzymatic activity. The lethal effects of snake venoms are probably due to the non-enzymatic proteins, though the enzymes and enzymatic combinations certainly contribute to the over-all toxicity of the poisons. In addition to the separate and combined activities of these substances, and the metabolites formed by their inter-reaction, the envenomated organism is capable of releasing several autopharmacologic substances which may complicate the mode of action of the venom, and may render treatment of the victim more difficult. The more important fractions of rattlesnake venom are crotoxin, crotactin and crotamine, rather than the enzymes noted in the book. Unfortunately, the authors have overlooked these generally accepted working hypotheses as well as the many splendid contributions on the physiopharmacology and chemistry of snake venoms by Habermann, Neumann, Frankel-Conrat, Goncalves, Moussatche, Slotta, Kaiser, Michl, Fischer, Raudonat and others. The "physiological fractions" outlined by the authors will no doubt shake-up many zootoxicologists working with the snake venoms. It is a common error for all of us to divide our limited knowledge into even more limited segments for the purpose of classification, or under the pretense of bidding for clarity. The arbitrary division of snake venoms into such classifications as neurotoxins, hemopathogens, cardiotoxins, hemotoxins, hemorrhagins, coagulants, anti-bactericidins, cytolysins, and some 40 other classifications given by various writers, is unfortunate. While these classifications may serve some useful purpose it is becoming increasingly

apparent from zootoxicological and chemical studies that neurotoxins can, and often do, have cardiotoxic and/or hemotoxic activity; cardiotoxins may have neurotoxic and/or hemotoxic activity; and hemotoxins may have the other activities, etc. Until the fractions responsible for the deleterious effects have been isolated and studied individually and in combination, one must consider all reptile venoms as substances capable of producing several important changes, sometimes concomitantly in one or more of the organ systems. The authors' survey of the chemical and zootoxicologic properties of venoms lacks a critical analysis of these problems and leaves much to be desired.

It will be a little disappointing to those who purchase the book with the thought of obtaining a balanced summary of the therapeutics of poisonous amphibians and reptiles to find that in the section on, "Medical Treatment in Cases of Snakebite," no data is given concerning the authors' personal experience with these injuries. As a result, many of the questions usually asked by physicians faced with the care of an envenomated victim have been overlooked. The data contained in the chapter deal with advice given by several competent physicians but the choice of material is, in the reviewer's opinion, sketchy and very partial. The condemnation of cryotherapy is unfortunate. The critical reader will find the references to unevaluated personal correspondence, used in support of various data, somewhat disconcerting.

It is true that there is no single volume dealing specifically with the material presented in this monograph. The excellent books by Klauber, Pope, and Kaiser and Michl provide most of the compiled information relative to this problem. The present volume should have its biggest appeal to campers, sportsmen and first aiders.—FINDLAY E. RUSSELL, Los Angeles County Hospital.

OBLIGATORY AND FACULTATIVE INSECTS IN ROSE HIPS. By W. V. Balduf. Illinois Biological Monographs, vol. 26. vi + 194 pages, 53 figures. University of Illinois Press, Urbana, Ill. 1959. Price, paperbound $3.50, clothbound $4.50.

This volume contains the results of a research project which extended over almost 30 years, but began with some casual observations. Dr. Balduf first became interested in the phenology of the rose curculio, *Rhynchites bicolor*, which he observed on the developing hips of cultivated roses growing on the University of Illinois campus. Later he observed some honey-yellow chalcids ovipositing in the rose hips in June. Seeking to discover something about the range of this chalcid, he picked some rose hips in northern Minnesota in September. When he returned to the university and opened the package of rose hips in October, he found that the hips had yielded neither weevils nor chalcids, but dipterous puparia. The following year in Minnesota he found a lepidopterous larva sharing the fleshy coat of rose hips with the dipteron.

He had, thus, found that rose hips in Illinois and Minnesota are inhabited by 4 species of phytophagous insects — later he found a second chalcid, which raised the total to 5. But these 5 phytophagous species proved to make up only a small part of the complex of species associated with the rose hip microcommunity. He embarked on an intensive investigation of the insects of rose hips, and this study produced 45 different species. Of these, 30 are directly associated with rose hips, while the other 15 are incidental.

The 30 species dependent on the rose hips are arranged thus: Phytophagous species which feed on the living substance of the hips, predatory and parasitic species which attack some stage or stages of the phytophagous ones, and scavengers which feed on the wastes left by those in the first two categories.

In all Dr. Balduf studied hips from 32 species or varieties of roses. Most of his rose material came from Minnesota, Wisconsin, and Illinois, but he also

secured rose hips from the area from Alaska, the Prairie Provinces, Ontario, and Maine in the north, south to California, Mississippi, and North Carolina. He reared over 14,000 adult specimens, and additional thousands of larvae, taken from the hips, were dissected to secure the immature stages of their endoparasites.

The bulk of the pages in this volume are devoted to careful, detailed studies of the habits and life histories of the individual members of the rose-hip complex. Dr. Balduf secured for study and description the eggs, larvae, and adults of almost all the species encountered in this investigation. Along with the accounts of these, a thorough coverage of the existing literature, if any, about them is given. Needless to say, almost all the information given in this study is new. Many of the insect parasites which he found had to be described before names for them were available for use in this book.

This volume includes a bibliography and excellent drawings of the adults and immature stages of most of the insects discussed in the text. The drawings are the work of Donald Van Horn.—B. D. Burks, Entomology Research Division, U. S. Department of Agriculture.

PLANT PROPAGATION: PRINCIPLES AND PRACTICES. By H. T. Hartmann and D. E. Kester. Prentice-Hall, Inc. 559 pp. 1959. $8.75.

This interesting and useful book provides, in the authors' words "a source of information concerning the fundamental principles involved in plant propagation and serves as a manual that describes useful techniques for propagating plants." The physiology and anatomy of seed selection, seed propagation, cutting, grafting, and budding are treated in separate chapters. Each chapter of more or less theoretical material is followed by one or more chapters of detailed descriptions of technique. The illustrations are numerous and well conceived, if rather small in execution. There are many references. The final section of the book considers briefly, too briefly, the particular techniques of propagation that are applicable to fruit and nut trees, to ornamentals, to annuals, and to herbaceous perennials.

The book apparently is intended primarily for a course in horticulture, and its material reflects the content of such a course. Botanically, the coverage of the book is far more limited than its sweeping title would indicate. Large groups of vascular plants are neglected, *e.g.*, the ferns and fern allies, the succulents, and the aquatics. There is no discussion of the propagation of thallophytes and bryophytes. The usefulness of the index suffers from an almost total exclusion of scientific names. It is easy to dwell on what is omitted and to praise what is included.—G. T. A. BENDA, University of Notre Dame, Notre Dame, Indiana.

A THOREAU HANDBOOK. By Walter Harding. New York University Press, 213 pp. 1959. $4.50.

This *Handbook* will prove invaluable to anyone who reads Thoreau with pleasure, as the plan of the book makes evident immediately. The book contains, first, a Thoreau chronology for ready reference, then five chapters entitled respectively, "Thoreau's life," "Thoreau's works," "Thoreau's sources," "Thoreau's ideas," and finally "Thoreau's fame," a study of the changing attitude toward Thoreau from his lifetime to the present. Each of these chapters is divided into two sections, the first of which provides a heavily, but unobtrusively, documented running account of the topic treated, and the second of which is a critical bibliography on that topic. These bibliographies include accounts of doctoral dissertations and some masters' theses which are not in print, and

in many cases provide brief summaries of the chief contributions of such works. In short, the book is a compendium of years of intensive Thoreau scholarship made available to anyone interested in Thoreau. More succinctly than any other source it defines Thoreau's present position in literary, scientific and political thought.

Naturalists are likely to be most interested in the chapter on Thoreau's ideas and discussion of his contribution to the science of his day and ours. Harding cites several uses of Thoreau's records by recent scientists, and adds that he understands that Thoreau's weather records in the *Journal* are even now being scrutinized by the American Meteorological Society. Harding feels that Thoreau, however much he protested against the confines of science as he knew it, became increasingly scientific in his concern with such data as species lists and water temperature records, and that his material has proved of value to modern scientists.

The bibliography included with this chapter is the fullest record of the evaluation of Thoreau's science yet printed; although the amount of space devoted to Thoreau as a scientist is small, as it should be, since Harding is interested in illustrating Thoreau as the multifaceted man that he was.

Probably Harding's major achievement in the *Handbook* is the objectivity and sense of proportion which the book reflects. The whole *Handbook* makes a determined effort to see Thoreau whole and avoid partisanship with any school of Thoreau interpretation. At the same time he sounds the necessary warnings that Channing's *Thoreau the Poet-Naturalist,* while it provides a great deal of source material, fails to properly identify quotations and is not always accurate in its facts; that Sanborn, who like Channing had the advantage of personal acquaintance with Thoreau and Concord, perhaps for that reason, felt free to alter Thoreau's writing to bring it into accord with his own standard of decorum; and that although Canby's biography added many new facts to our knowledge of Thoreau, his assertion that Thoreau was unconsciously in love with Lidian Emerson rests upon unscholarly evidence.

In view of the widespread disagreement as to whether or not Thoreau's life proved ultimately satisfying to him, it is important to note that Dr. Harding who is conspicuously without "a chip on his shoulder" or "a thesis in his hand," whose Thoreau work has been both extensive and remarkably free of the curse of thesis, records that "Canby looked upon Thoreau as the happiest man of the Concord group. It is my opinion that Canby is closest to the truth on this point," and on page 167 he writes "Basically Thoreau's life was a happy one."

The chapter on "Thoreau's Fame" will be of interest to naturalists chiefly because it demonstrates how recently interest in Thoreau as a scientist has developed. — KATHRYN AND PHILIP WHITFORD, University of Wisconsin, Milwaukee.

A REVIEW OF THE SIRENIA AND DESMOSTYLIA. By Roy H. Reinhart. University of California Publications in Geological Sciences, Volume 36, No. 1, 146 pp., 19 figs., and 14 plates. 1959. $3.00.

Reinhart has apparently devoted a great deal of time and energy to this fairly extensive revision of the orders Sirenia and Desmostylia. All Sirenian fossils reported from the east and west coasts of North America, from the Caribbean and the west coast of Mexico are reviewed, and the more important European and Egyptian specimens are compared with the Western Hemisphere forms. It is shown that the family Dugongidae has had a world-wide distribution in the past and that the family has experienced a moderate diversity of form as compared to that found in the family Trichechidae. Reinhart's suggestion that the family Dugongidae was early split into two phyletic lines start-

ing with the middle Eocene *Eotheroides* is quite reasonable.

It is indeed gratifying to see a paleontological publication in which the truly indeterminate nature of much of the sirenian material from eastern United States is regarded as such. The stratigraphic and correlational problems associated with the Ashley River beds of South Carolina and the Calvert formation of Maryland are adequately emphasized. However, it is unfortunate that the author, in discussing the Dugongidae of Florida, does not mention a similar problem in regard to sirenian remains from the Bone Valley Gravel formation of west central Florida. At least some faunal elements of the entire assemblage of vertebrates obtained from this formation are definitely Miocene, while others seem to be Pliocene. In addition, superficial beds have yielded well-known Pleistocene forms. Most of the marine vertebrates from the formation appear to be Miocene in age while most of the terrestrial forms are presumably Pliocene. Thus, the Bone Valley Gravel felsinotheres may be Miocene rather than Pliocene. It is also unfortunate that, although the type locality of almost all of the more important fossil specimens is given, there is no locality or formation mentioned in reference to either *Felsinotherium ossivalense* or *F. floridanum*.

It may have been a little easier for the reader had the author not interspersed his discussion of the known sirenian fossils of various areas in the New World with descriptions of new genera and new species. It is also unfortunate that in a monograph of this scope the Order Desmostylia is not as thoroughly reviewed as the Order Sirenia. *Cornwallius* might have been profitably discussed in somewhat more detail. Reinhart gives a very fine synopsis of the familial and sub-familial characteristics of the various groups included within the Order Sirenia. It would have been to some advantage to have had a similar synopsis of the familial characters of the Desmostylia at the end of that section. He might also have included a more thorough discussion of the evidence bearing on the advisability of erecting a new order of mammals. No true diagnosis of the order exists in the review, and the reader must refer to a previous single-paged paper published six years ago in the *Journal of Geology*.

The drawings throughout are well-chosen with respect to position and are well executed. On the whole the plates are very good, although some of the elements, particularly several of the more important limb bones of *Desmostylus* and/or *Vanderhoofius* might have been shown to better advantage in line drawings.

New taxons described include *Caribosiren turneri*, n. gen. et sp., *Halianassa vanderhoofi*, n. sp., *Vanderhoofius coalingensis*, n. gen. et sp., and *Paleoparadoxia tabatai*, n. gen. All previously described species of *Desmostylus* are placed in the synonymy of *D. hesperus*.

The publication is quite thorough, and provides considerable evidence that Reinhart is well qualified to judge the systematic value of the distinctive characters of the described forms. Although the specialist may find a few points with which he disagrees, the monograph is most certainly a valuable contribution to our knowledge of these Tertiary marine forms. — WALTER AUFFENBERG, University of Colorado, Boulder.

THE PHENOMENON OF MAN. Pierre Teilhard de Chardin. Harper & Brothers. 318 pp. 1959. $5.00.

There is something stimulating in perusing a book that has been suppressed; perhaps that is one of the reasons *The Phenomenon of Man* seems more noteworthy than similar volumes dealing with the evolution of life that recently have been published. Frankly teleological and concomitantly monistic, the manuscript was composed by the Jesuit paleontologist, Pierre Teilhard de

Chardin, during the years 1938-1940. However, his religious superiors thrice forbade publication of this document, although he did publish other works until his death, notably *Le Groupe Zoologique Humain* and *La Vision du Passe.* Fortunately, Père Teilhard left his manuscripts to a friend so that the book could be released after his death in 1955 when permission to publish was no longer required. Originally published as *Le Phenomene Humain* in France where it was the best-selling nonfiction book of the year 1955, the English version has been expertly translated by Bernard Wall.

In an attempt to produce a synthesis of the emergence of life which will culminate in the sharing of all life in the Omega, which is the end point of evolution according to Père Teilhard, both the biological and psychical development of nature is considered. All matter is held to possess a certain degree of consciousness. This consciousness emerges more distinctly in the instincts of man and achieves its climax in the human organism with the appearance of reflective thinking. Man, however, is not merely a more highly individualized organism. Man is a person — one who has transcended individuality in personality.

This individualization and personalization depends on the cephalization of the unfolding organism, since it is the head that contains the main organ of coordination or brain. As Sir Julian Huxley points out in the introduction, Père Teilhard stresses that the process of evolution on earth is itself now in the process of being cephalized. Evolution is at last becoming conscious of itself in that man is the first product of evolution to appreciate the very process which has developed him. But in man evolution is characterized more by cultural than genetic or biological change. Therefore, our concept of evolution has to include what is termed a "psychosocial process." This is a complex of factors which have produced cultural differentiation. Various groups resulting from this process are not considered as sharply delineated as biological species. Man is the only successful type of life to remain a single interbreeding group. Today there is a tendency towards cultural convergence resulting in a movement of the whole human species into a single interbreeding group based on a unitive, self-developing framework of thought — the noosystem. (Gr. *noos* — thought.) From this the author expands his concept to that of a noosphere or thinking membrane with which man has overlaid the biosphere or life layer of the earth. The noosphere incorporates the cosmos, including its trend in direction and time, as well as the psychosocial processes existing on earth. This makes of the noosphere a microcosm, including both the knowledge of the universe as well as the unification, with increasing intensity, of the system of human thought. And this will result in the Omega point, where the noosphere will achieve its essential unity and become a hyperpersonal organization.

Indeed, this volume requires more than ordinary concentration to grasp, particularly since the author is prone to sentences which are occasionally almost a page in length. At other times, what appear at first glance to be merely disjointed phrases are interspersed among the elongate sentences. Yet, *The Phenomenon of Man* is a remarkable integration of evolutionary data with religious principles and certainly is worth the effort needed to thoroughly digest its contents. Since there are reputed to be three more books of Père Teilhard's yet to be published, we can hope that these will clarify some of the unique concepts that are embodied in *The Phenomenon of Man.*

The epilogue entitled "The Christian Phenomenon" should more properly be reviewed by a competent theological authority, since some of its conclusions are as unusual as the opinions expressed in the preceding chapters.—BROTHER G. NICHOLAS, F.S.C., Department of Biology, University of Notre Dame, Notre Dame, Indiana.

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Studies Concerning the Effects of Nutrition on Morphology of Amebas. I. Mayorella cultura Bovee, on Abundant and Starvation Quantities*

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Students of the morphology and taxonomy of the naked, lobose amebas of the order Amoebida (Hall, 1953) have long been aware that various ecological conditions might be construed to cause morphological variations such that classical methods of taxonomic discrimination [i.e. use of pseudopods (Schaeffer, 1916, 1926) which are dependent on locomotive activities] may not always be wholly reliable (Bovee, 1953; Jepps, 1956; Leidy, 1879; Mast, 1928; Penard, 1902; Schaeffer, *loc. cit.*).

Thus some researchers have attempted to dismiss from consideration all ameboid morphologies other than those of the nuclei or the mitotic variations thereof, deeming mainly the nuclei to be of taxonomic value (Calkins, 1907; 1913, 1926; Hyman, 1940; Jepps, *loc. cit.;* Kudo, 1952, 1954, 1959; Minchin, 1911; Reichenow, 1953; Singh, 1952; Wenyon, 1926).

Physiological tests of some stringency beyond normally encountered limits have produced results (Brinley, 1928; Daugherty, 1937; Edwards, 1924; Hopkins, 1928; Jennings, 1906; Kriszat, 1952; Mast, 1928, 1929; Morita and Chambers, 1929; Nardone, *et al.*, 1956; Neresheimer, 1905; Pantin, 1926; Ray and Hayes, 1954; Reznikoff and Chambers, 1927; Seifriz, 1939; Verworn, 1903) which sometimes are quoted (or occasionally misquoted) by critics of locomotive taxonomic criteria in support of their complaints, thus further confusing the problem.

Despite the criticisms from all such sources, little has been done to find whether and to what extent, ecological variations normally encountered by amebas might affect locomotive morphologies and therefore their taxonomic utility.

We[1] have been able to grow clonal cultures of a small ameba of

* Supported by NIH Research Grant E-1158, and the University of Florida.
[1] I wish to express my thanks to Mrs. Jacqueline Hynes, who, as my research associate, developed the techniques of clonal and axenic cultures herein described; and who brought to my attention the apparent effects of starvation on these amebas.

stagnant freshwaters, *Mayorella cultura* (Bovee, 1960) which forms locomotive pseudopods of the clear, conical, determinate shape characteristic of the family *Mayorellidae* Schaeffer 1926. These we have tested on abundant and on starvation quantities of food, and have observed the effects on its locomotive morphologies.

MATERIALS AND METHODS

The ameba was found in a water sample collected June 26, 1957, at the shaded south shore of a small lake ("Bivin's Arm") at the southern periphery of Gainesville, Florida. There was much aquatic vegetation (*Elodea, Potomogeton, Lemna*) and vegetable detritus at the site. The water temperature was 27° C.; pH was about 6.5.

At the time the ameba was first seen on July 24, 1957, the temperature of the water sample was 22° C., and pH again somewhat acid, at 6.4.

The microscope slide bearing the water droplet and the cover slip were placed separately, wet side down, upon sterile, nutrient Cerophyll-agar (Bovee, 1959a) in a covered Petri dish, and incubated at 22° C. for five days. Amebas then feeding on native bacteria were numerous, as were the bacteria. Transfers were made thereafter at 10 to 12 day intervals, and an overlay of aqueous saline (Neff, 1957) added. The cultures were flourishing by mid-December 1957.

On January 31, 1958, clonal cultures were established by transfer of individual cysts to non-nutrient agar plates to which 0.2 ml. of antibiotic mix had been added to inhibit bacterial growth (200 mg. penicillin and 200 mg. streptomycin in 10 cc. of distilled water).

From one of these clones during February 2 to 5, 1958, other clones were established on four other agar plates: (1) nutrient cerophyll agar; (2) nutrient cerophyll agar with liquid overlay of 5 cc. of Neff's ameba saline; (3) non-nutrient agar; and (4) non-nutrient agar with liquid overlay. All four types of cultures were also established with the antibiotic mix *addendum* which restricted the bacterial rate of increase to a low order, but did not appear to affect the amebas.

Observations were made over a period of about two weeks, until practically all the trophic amebas had encysted, then excysted, and once more encysted.

A Bausch and Lomb phase contrast microscope was used at 200× for observation of the mayorellas on the agar plates. An American Optical-Baker interferometer microscope with shearing-focus condensors and objectives at 100× and 400 × was used for detailed observations of morphology; the amebas were studied after transference to a drop of Neff's ameba saline on a clean glass slide, and covered with a clean cover slip.

Light was provided by a Bausch and Lomb research-type microscope lamp model 31-26-33, with or without ground-glass, "daylight blue," sodium-green, and heat-filtering glass filters, singly or in various combinations.

Measurements of amebas were made at 200× with the phase contrast, and at 400× with the interferometer system, by means of a calibrated ocular micrometer.

The pH was controlled within narrow limits by the employment of Neff's buffered ameba saline both in the liquid component of the agar, and as the liquid overlay where used. The pH of the agar thus prepared was 6.4, and that of the saline, 6.5. Oxygen was continually available to the amebas since the petri dishes were kept covered but not sealed.

Inoculations and transfers were made by standard, sterile bacteriological techniques with a wire loop of nichrome alloy. Media were prepared by standard bacteriological methods. Individual cysts were picked out with sterile glass micropipettes and transferred.

RESULTS AND OBSERVATIONS

Both bacteria and amebas grew abundantly and continuously during the observation period on the cerophyll-agar either with or without overlay. The antibiotic mix somewhat slowed bacterial growth when added to the cerophyll media, but there was always enough bacterial food for the amebas. The cerophyll extract, proteose-peptone, glucose and salts in the agar provided an abundant nutritive *quantum* for the bacteria.

On the non-nutrient agar, which contained only added salts and water, even with the overlay, bacterial growth was very slow; and was even slower on that which contained the antibiotics. On the latter, after four days, only a few amebas were present. These remained upon or at the periphery of the few small colonies of bacteria, feeding upon them. A few amebas and bacteria were present until about seven days after clonal establishment. In eight or nine days only an occasional trophic ameba was found, a few encysted amebas and very few bacteria.

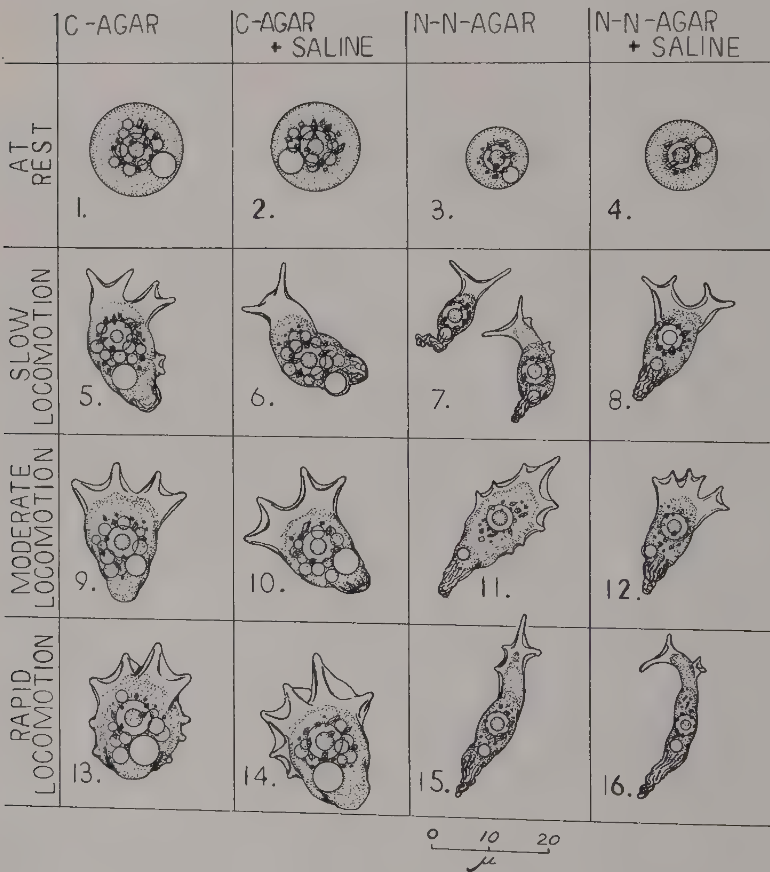
It was no surprise to observe that well-fed amebas on nutrient-cerophyll agar appeared plump, with many glistening globules of stored nutrients in the cytoplasm; whereas the less well-fed amebas and semi-starved animals on non-nutrient plates were progressively leaner.

The conical pseudopods, which are thrown forward in pairs, were approximately the same lengths in the well-fed and semi-starved amebas. However, the thickness of the pseudopods varied considerably. In the nutrient-cerophyll agar without liquid overlay, pseudopods extended by the amebas were 2 to 3 μ in diameter at the bases, tapering to rounded tips 1.5 to 2 μ in diameter (Figs. 5, 9, 13). On cerophyll agar with liquid overlay pseudopods of the amebas were 1.5 to 2.5 μ in diameter at the bases, and 1.25 to 1.5 μ in diameter at the rounded tips (Figs. 6, 10, 14).

On non-nutrient agar without liquid overlay, the amebas extended pseudopods which were 1.2 to 1.4 μ in diameter at the base and 0.8 to 1.0 μ in diameter at the tips (Figs. 7, 11, 15); on liquid-overlaid

non-nutrient agar, the amebas developed pseudopods 0.8 to 1.2 μ in diameter at the bases and 0.6 to 0.8 μ diameter at the tips (Figs. 8, 12, 16). In all cultures pseudopods measured 2 to 8 μ long, the longer pseudopods being slightly larger in diameter at bases and tips than were the shorter pseudopods (Figs. 11, 13, 14, 15, 16).

Some variation in size was noted for the more or less ovate bodily mass. This mass was usually broader, and blunter near the anterior wave and the rear in well-fed amebas (Figs. 13, 14). It was more slender and elliptical in semi-starved amebas, often with a somewhat



Figs. 1-4.—Resting forms of *Mayorella cultura* in the indicated media. Figs. 5-16.—Various locomotive forms on the indicated media. C — agar = nutrient agar with "cerophyll" extract; C — agar + saline = nutrient agar with "cerophyll" extract, overlaid with Neff's saline; n-n-agar = non-nutrient agar; n-n-agar + saline = non-nutrient agar overlaid with Neff's saline.

attenuated and wrinkled rear end, so that the starved amebas appeared longer (Figs. 7, 12, 15). Actual over-all length varied little, being 2 to 4 μ more for the starved amebas in rapid locomotion, due almost entirely to the attenuation of the contracted rear end.

The ratio of length/width, however, varied greatly for well-fed amebas *versus* semi-starved ones.

The average length/width ratio (all stages of locomotion) for the granular body mass, using the measurement of length from the rear end (at the base of the attenuated "tail," when present) to the border of the anterior clear portion from which pseudopods extend, divided by width at the broadest part of the granular bodily mass, was 1.42 for the well-fed amebas, and 2.20 for the semi-starving ones. Total length and total width were not employed, since pseudopods, in some stages of changing directional pathways, may be extended at both ends, or around the periphery (or a considerable portion thereof), producing less reliable measurement and ratio.

Giant forms occasionally appeared, usually on antibiotic-free, non-nutrient agar without overlay, when most of the amebas were encysted, and bacteria were available, but sparse. These giants were about 50 percent longer and broader than the average, otherwise normal in appearance and activity; but they did not encyst, and later died.

In locomotion the mayorellas progressed by throwing pseudopods forward in pairs above and to left or right (usually alternately) of the previously formed pair, so that a zig-zag, or wavy pathway was developed. One pseudopod of each pair was longer than the other, the longer one usually extended almost directly along the existing path of progress, the shorter at an angle usually between 60° to 90° to right or left of the existing pathway (Figs. 5, 6, 7). Older pairs of pseudopods themselves contracted, and were pulled laterally by contractions of the bodily mass, being reincorporated therein before the main part of the bodily mass passed their positions of adherence to the glass slide (Figs. 7, 13).

In slow movement, and in slow locomotion, the pseudopods of each pair were more nearly of the same lengths than in more rapid advance, and were less quickly contracted and reconstituted into the bodily mass (Figs. 10, 12).

Each pseudopod was connected to its partner of the pair by a clear web, of greater or lesser extent, particularly in more rapid locomotion (Figs. 11, 12, 13, 14).

In general, the more slender pseudopods of semi-starved amebas showed greater disparity of length between the two members of the pair than did the heavier pseudopods of the well-fed amebas (Figs. 15, 16). For the starved amebas in rapid locomotion the longer pseudopod directed along the pathway of locomotion measured 2 to 3 times as long as the shorter member directed angularly away from the locomotive path (Figs. 15, 16). Also, the angle between the bases of the pseudopods of the pair for the starved amebas was usually 70°

or more in spread, often as much as 90° (Fig. 15) and sometimes, in rapid advance, forming obtuse angles to 120° (Fig. 16). As a result such amebas appeared on cursory examination to be monopodal.

The well-fed amebas formed pseudopodal pairs which usually diverged from 60° - 80° (Figs. 9, 10) only occasionally as much as 90° (Figs. 6, 14), and were not seen to form obtuse angles. For both starved and well-fed amebas, those on the liquid-overlaid agar tended to throw pseudopodal pairs slightly more angularly divergent than their equivalently fed counterparts on non-liquid-overlaid surfaces. The clear web connecting the pseudopods of a pair rarely joined more than 5/8 the lengths of the newly-formed pseudopods of the well-fed amebas; but connected 2/3 to 3/4 of the lengths of such pseudopods of semi-starved ones, particularly in moderate locomotion (Figs. 11, 12). On liquid-overlaid media slightly more of the lengths of pseudopods of a pair were connected by the clear web then for amebas grown on non-liquid-overlaid agar (Figs. 10, 11, 12).

The rates of locomotion at 22°C. for the well-fed amebas were slower than those of the semi-starved mayorellas. In general, the well-fed amebas on cerophyll agar surfaces without liquid overlay moved slightly less than the over-all length of the body in one minute, averaging about 19 to 20 μ per minute when advancing steadily. Well-fed organisms on the cerophyll agar with liquid overlay moved a bit faster, 20 to 22 μ per minute, with frequent turns. Semi-starved amebas moved more rapidly forward, 25 to 28 μ per minute on non-overlaid agar, and 27 to 30 μ per minute on the liquid overlaid agar.

Severely-starved, emaciated amebas, conversely, moved very slowly, becoming very elongate, halting frequently before resuming progress. In short periods of steady advance only 8 to 12 μ would be traversed by such organisms per minute.

Locomotion by these mayorellid amebas was usually along the border of the streak where bacterial colonies were present. When several bacterial streaks were present on the same plate, little, if any, migration from one streak, or one colony along a streak, to another was evident, either by well-fed or poorly-fed amebas. In the few instances where amebas did wander away from the bacterial source, well-fed individuals soon extruded much of the stored globular materials, and encysted; while starved individuals which wandered away from the bacterial streaks became emaciated and inactive, and either died or formed small cysts.

Encystment occurred when there was a lack of bacteria available for food *in the immediate vicinity* of the ameba. On nutrient-cerophyll-agar plates the bacteria grew abundantly along the streaks where inoculated, and large numbers of amebas developed and migrated along the streak. Those which were prevented from reaching the bacteria for a few hours because of the dense aggregation of amebas, then encysted. Active trophic amebas were found, usually, no farther away from the bacteria than about 150 μ.

Excystment usually occurred when new colonies of bacteria de-

veloped, probably from bacterial spores in fecal wastes of the amebas among the clumps of cysts. It was under such situations that the "giant" amebas, previously mentioned, developed.

There appeared to be some correlation in nuclear volume and cytoplasmic volume. Resting, well-fed amebas (with many food globules) measured 16 to 18 μ in diameter in spherical form, the nucleus being spherical, 6.5 μ diameter, and the spherical nuclear endosome 3.2 μ diameter (Fig. 13). Semi-starved and newly excysted amebas measured 8 to 10 μ in spherical diameter, the nucleus being 3.5 μ diameter and the nuclear endosome 1.6 μ diameter (Figs. 15, 16.) When encysted, the spheroidal cytoplasmic mass was 8 μ diameter, the nucleus 3.2 μ diameter and the endosome about 1.5 μ diameter. Only one functional contractile vacuole appeared in any of the amebas under the various conditions employed.

In general, the major changes accompanying the progress of starvation were a loss in volume, more slender outlines in locomotion, and more slender, and slightly shorter pseudopods. The formation of pseudopods (and their conical, clear structure, rounded at tips) in pairs, more or less connected by a clear wave, did not change sufficiently to produce any error in the identity of the ameba as a species. Moreover, the pseudopods clearly were those characteristic of this species so long as the amebas moved about actively and fed successfully.

Discussion

The fiction that the gross morphologies of any ameba and of its pseudopods are subject more to the vagaries of ecological conditions than to the metabolism of the organism perhaps began with the surface-tension theories of ameboid locomotion (Berthold, 1886; Bütschli, 1892; Rhumbler, 1898; Verworn, 1903); and failed to die with them. This fiction has been further perpetuated by Verworn's (*loc. cit.*) account of "changing" the "species" of ameba from "limax" to "radiosa" by addition of KOH to the water containing the organism. This fantastic misinterpretation by a great man of the results of his experiment has been regurgitated into most textbooks of protozoology as a warning against the employment of pseudopods and locomotive morphologies as taxonomic criteria for amebas (Calkins, 1926; Hyman, 1940; Jepps, 1956; Kudo, 1954; Minchin, 1912; Reichenow, 1953; Wenyon, 1926).

Environmental conditions supposed to be influential in obviating control by the ameba of its own morphology of bodily mass and pseudopodal forms include cations and anions, gross pH, O_2 and CO_2 tensions, light, temperature, pressure, and organic materials (particularly dissolved or colloidal, or as food).

Claims that gross form of the amebas (*i.e.* from "limax" to "radiosa") (Scheel, 1899) may be controlled at will by cations (Spek, 1925; Verworn, 1903) or that cations produce a monopodal form (Edwards, 1924), a contracted form (Brinley, 1928), or "Ca", "Mg" or "Ba" forms (Pantin, 1926) have been dismissed (Mast, 1928). Observations

show that locomotor processes in amebas are *not* dependent upon substances in solution in the water, but are regulated internally (Mast, *loc. cit.*). A radiate form is assumed in distilled water, or weak HCl at pH 5 to 6, in NaOH at pH 7.6 to 8, or in N/500 to N/100,000 concentrations of the chlorides and sulfates of Na^+, K^+, Ca^{++}, and Mg^{++}, or mixtures of these salts, in urea, and lactose solutions; followed *in each case* by a descent to the slide, then development of lobose, and, finally, monopodal ("limax") forms (Mast, *loc. cit.*). Other observations show that there are cycles of activity(Bovee, 1949) and growth (Bovee, 1953; Prescott and James, 1955) in a 24-hour period which produce similar sequential forms.

A like array of forms results from physical disturbance of the water and of the amebas (Bovee, 1953; Jennings, 1905; Mast, 1928; Schaeffer, 1921).

Low or high O_2 tensions cause rounding up, death and disintegration, except for brief exposures (Hulpieu, 1931) which cause the adoption of a temporary monopodal form. Increase of CO_2 similarly causes contraction and death, except in brief, non-lethal exposures (Reznikoff and Chambers, 1927); and injected bubbles of CO_2 gas cause some temporary damage followed by the assumption of the monopodal form (Reznikoff and Chambers, *loc. cit.*).

Temporary monopodal forms also develop in strong light (Prescott, 1956), or in low intensities of light (Mast and Stabler, 1937), sudden change of temperature (Hopkins, 1937b), weak direct electrical current (Angerer and Wilber, 1943), or starvation (Prescott, *loc. cit.*). After adjustment, or during and after feeding, lobose or discoidal forms reappear.

Severe experiments which approach lethality for the amebas result in a "rounding-up" of the ameba, followed by recovery if sub-lethal.

Centrifugation up to 149$\times$ gravity is followed by complete recovery (Murphy, 1940). High, hydrostatic pressures of 6,000 lbs./sq. in. are withstood, with recovery in 5 minutes (Marsland, 1956). Amputation of practically all the cytoplasm causes amebas to round up; but is often followed by complete recovery of specific identity (evidenced by normal movement and feeding) in 24 to 48 hours (Phelps, 1926; Prescott, 1956; Willis, 1916). Ultrasonic churning of the cytoplasm does not particularly disturb normal locomotion (Schmitt, 1929); and sublethal shocks of alternating current produce no permanent change (Angerer and Wilber, 1943); nor do sub-lethal vital stains (Torch, 1955); nor temperatures to 40° C. (Hopkins, 1937b; van Herwerden, 1927).

Lethal orders of salts (Brinley, 1928), HCl (Morita and Chambers, 1929), electric shocks (Englemann, 1869; Kuhne, 1864), high pressures (Marsland, 1956), and vital stains (Torch, 1955) all produce deformation, and/or coagulation and contraction to spherical form, destruction of the plasmalemma and disintegration. Surfactants tend to be toxic, and cause shrinkage of the bodily mass and pseudopods, plus blistering (Nardone, *et al.*, 1956).

In general, amebas respond to changes of a chemical or physical nature usually in one of three ways: (1) the assumption of a floating radiate stage; (2) the shift to a temporary monopodal form (usually characteristic of rapid locomotion); or (3) contraction to discoidal or spherical form reducing surface area. If the environmental change is sublethal, adjustment is made and normal activity resumed. If the environmental change is lethal, contraction, moribundity, death and disintegration follow.

Sublethal changes in the environment cause the assumption of a normal defensive morphological pattern. They do *not* materially nor permanently alter the nature of movement of the amebas nor their pseudopodal characteristics. In fact, any change in the coordinated pattern (Schaeffer, 1921) rate or type (Schaeffer, *loc. cit.;* Seifriz, 1939) of locomotion may be pathological. Form in coordinated locomotion is a criterion of normality (Schaeffer, *loc. cit.*; Seifritz, *loc. cit.*) and of taxonomic distinction (Bovee, 1949; Schaeffer, *loc. cit.*).

The surface over which the ameba moves is said by some observers to affect the form taken by an ameba (Hogue, 1917; Neff, 1958). Difficulty of attachment and movement have been noted on paraffin, quartz, and pyrex as compared to optical glass (Mast, 1928). "Walking" forms have been recorded (Bovee, 1953; Dellinger, 1906; Wilber, 1946), and other variations of movement on plant surfaces (Leidy, 1879; Penard, 1902). Density of agar in the culture medium is also said to affect form (Hogue, *loc. cit.*); as well as the depth of water film over the agar surface (Neff, *loc. cit.*). These observations, however, mostly represent experimental laboratory conditions and cannot obviate the facts that when crawling in water on a wet glass surface, (or any other surface) the patterns of locomotion adopted by any ameba on that type of surface are *characteristic of that ameba on that surface,* and of no other kind of ameba on that or any other surface.

Starvation affects mainly the size of the ameba (Andresen, 1956; Andresen and Holter, 1955; Johnson, 1930; Mast and Hahnert, 1935; Prescott, 1956) and perhaps the length of its pseudopods (Mast and Hahnert, *loc. cit.;* Short, 1946). Overfeeding affects principally the bodily size and relative diameter of pseudopods (Mast, 1939; Mast and Hahnert, *loc. cit.*). Kind of food, if adequate, has little if any effect on the pattern or the rate of locomotion (Hopkins, 1937a), but may produce temporary bipodal or monopodal forms (Short, *loc. cit.*), or a few more somewhat thinner and flatter pseudopods which are due more to the culture supplement (wheat or hay) then to the kind of food animal devoured by the ameba (Short, *loc. cit.*). No significant differences affecting bodily form result from digesting any one of a variety of food organisms, whether any one of them may be nutritionally adequate, inadequate, or toxic, so long as the amebas are able to move and feed (Andresen, *loc. cit.*; Mast and Hahnert, *loc. cit.*). Food taken by pinocytosis may affect bodily volume, but not form nor movement (Chapman, Andresen and Prescott, 1956).

It is highly important, as well as merely interesting, that in the

numerous papers written about experiments or studies on amebas very few of the observers or experimenters have noted any significant changes in form or activity of the amebas, so long as the conditions were sub-lethal.

It is doubly important that such changes were not reported, since they are exactly the criteria most sought for to determine experimental effects. Had such changes occurred, they are certain to have been seen and recorded; not overlooked, nor ignored, nor omitted.

In short, amebas react to and adapt to sub-lethal environmental changes, developing characteristic defensive morphological patterns which are a part of the adjustment; then, after a time, they resume normal and characteristic activity. Their adjustment to extra food is enlargement — in other words, they get "fat," and "clumsy." When starved they shrink and become lean ("monopodal") in locomotion.

So long as they are able to move in coordinated fashion (*i.e.* are not moribund) amebas retain and maintain their specifically identifiable bodily and pseudopodal morphologies, which are in turn related to and the result of their internally directed and coordinated metabolic and locomotive functions.

SUMMARY

Mayorella cultura Bovee (1960) has been grown in clonal cultures on media providing adequate nutrients for the bacteria serving it as food, and in bacteria-free clonal cultures in nutrient liquid media. It has also been maintained on non-nutrient media inadequate for either the bacterial or ameboid growth.

On the adequate media it becomes larger, and bulkier, with well-defined pseudopods; and on the inadequate media, emaciated. The characteristics of locomotive patterns are relatively undisturbed so long as the amebas are not moribund. It is concluded that locomotive patterns and pseudopodal forms are valid taxonomic criteria.

A survey of the literature concerning the effects of experimental and ecological conditions other than nutritive conditions indicates that for amebas, generally, these conditions do not particularly disturb the patterns of morphology and/or locomotion, so long as the experimental and ecological conditions are sublethal, and so long as the amebas are not moribund, and are able to move and feed in coordinated fashions. For amebas generally, as well as for *Mayorella cultura,* it is concluded that morphological patterns of the whole body and the pseudopods formed by it in locomotion are useful and valid taxonomic criteria.

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The Cyperaceae of Illinois. I. Cyperus

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This is the first in a series of studies concerning the family Cyperaceae in Illinois. It is intended to define the species within each group, to give synonymy, to supply keys for identification of the species, and to show distribution of the species in Illinois. Line drawings of the diagnostic characters of each group will be presented. In order of their appearance, the parts of the study will be: I. *Cyperus;* II. *Dulichium* and *Eleocharis;* III. *Bulbostylis, Fimbristylis, Fuirena, Hemicarpha,* and *Lipocarpha;* IV. *Scirpus* and *Eriophorum;* V. *Rhynchospora, Cladium,* and *Scleria;* and VI. *Carex.*

Herbaria which have made their collections of *Cyperus* available for this study are those of the Illinois State Museum (ISM), Illinois Natural History Survey (ILLS), Chicago Museum of Natural History (F), University of Illinois (ILL), Missouri Botanical Garden (MO), Eastern Illinois University (EI), Western Illinois University (WI), and Southern Illinois University (SIU). Much appreciation is accorded Mr. Don Drapalik who prepared the distribution maps and helped with the annotations.

History of the Genus

The genus *Cyperus* is a difficult group taxonomically which has rather poor species delimitation in Illinois as well as most of eastern United States. Many of the species show much variation, and considerable intergradation takes place among others.

Kükenthal has been an ardent student of *Cyperus,* and his monograph (1936) is foremost among those for the genus. Fernald and others, however, have pointed out numerous inconsistencies and errors so that Kükenthal's treatment should be studied critically before being followed.

Traditionally, *Cyperus* has been divided into other genera or subgenera based upon characteristics of the rhachilla, scales, number of stigmas, and achenes. The differences between some of the groups are rather difficult to observe and are based on somewhat tenuous characters.

Kükenthal recognizes six subgenera with only the subgenus *Juncellus* not being represented in the Illinois flora. Linnaeus (1753) listed several species of *Cyperus* to form the groundwork for future study of the genus. Other extensive works relating to North American species of *Cyperus* were by Rottboell (1773), Vahl (1806), Torrey (1836), Boeckeler (1868; 1870), Britton (1886), and Clarke (1883;

1884; 1898; 1903). In recent years, O'Neill's studies have contributed much to the present knowledge of North American species of *Cyperus*.

The name *Mariscus* has been applied to several species of rushes and sedges from the time it was first used by Pliny (77 A.D.) until Gaertner applied it to a group of plants which he related to the genus *Cyperus* in 1788. Since Vahl's work in 1806, *Mariscus* has been used as a subgenus of *Cyperus* or as a distinct genus, but this latter usage is prohibited since Zinn (1757) described a species belonging to *Cladium* under the genus *Mariscus*.

O'Neill (1942) has discussed thoroughly the reasons either for maintaining *Mariscus* as a subgenus of *Cyperus* or segregating it as a distinct genus.

The genus *Kyllinga*, created in 1773 by Rottboell and maintained in this rank by such workers as Vahl, Boeckeler, Clarke, and many recent authors (Jones, 1950; and others), was treated as a subgenus by Suringar in 1898, a rank which I propose to maintain for this taxon.

MORPHOLOGY OF THE ILLINOIS SPECIES

The species of *Cyperus* are cespitose annuals from fibrous roots or perennials with short rhizomes bearing corm-like swellings or with long scaly rhizomes (*C. esculentus*). In *C. esculentus*, the rhizomes sometimes give rise to edible swollen tubers. These tubers are frequently absent from herbarium specimens because they are easily lost in digging.

The culms range in size from depauperate specimens of *C. strigosus* which may be as small as one centimeter to robust specimens of *C. erythrorhizos* which may become nearly one-and-one-half meters tall. The culms may be wiry and very slender (*C. filiculmis* var. *macilentus*) or nearly one centimeter broad in several species. They are either glabrous or retrorsely scabrous beneath the inflorescence.

The leaves are flat or involute, rarely conduplicate, glabrous or sometimes scabrous on the margins, 0.5-12.0 mm broad, much surpassing or shorter than the culms.

The inflorescence, known as an anthela, is composed of 1-several sessile compact heads and frequently with 1-several simple or compound rays which may become 10 cm long. The inflorescence is subtended by 1-several involucral bracts, some of which usually greatly surpass the inflorescence. These bracts are flat or rarely involute, glabrous or scabrous along the margins.

The spikes may be cylindric, ellipsoid, oblongoid, or globose, with five to very numerous spikelets either radiating in all directions, horizontally spreading, ascending, or rarely reflexed (*C. lancastriensis*).

The spikelets are very flat to terete, linear to lanceolate, rarely falcate in some specimens of *C. erythrorhizos*, one- to forty-flowered, to 35 mm long, 1.0-3.5 mm broad, obtuse or subulate.

Scales vary in color from stramineous to strongly marked with

purple, loosely to tightly imbricate, or with the scales remote in *C. engelmannii,* narrowly oblong, lanceolate, ovate, or rotund (*C. houghtonii*), obtuse to acute or acuminate and outwardly recurved in *C. acuminatus* and *C. aristatus,* sometimes mucronulate or with a mucro to 1.5 mm long, obscurely or conspicuously one- to fifteen-nerved, 1-5 mm long. The rhachilla which is occasionally exposed between the scales may be broadly winged or wingless.

There are 1-3 stamens per flower. The stigmas are two- or three-cleft, sometimes nearly to the base, frequently early deciduous, rarely persistent and protruding up to 4 mm in *C. diandrus.*

The achenes are lenticular or trigonous, rarely flattened, stramineous to fuscous to black, narrowly linear to broadly ovate, sometimes with tranverse wrinkles (*C. flavescens*) or minutely pebbled (*C. aristatus*), obtuse or apiculate, 0.5-3.3 mm long.

Geographical Considerations

Kükenthal (1936), summarizing the geographical distributions of *Cyperus,* listed 40 species from Atlantic North America of which 18 were known from Illinois. (The nineteenth Illinois species, *C. grayioides,* which recently has been described, was unknown of course to Kükenthal).

The majority of the Illinois species has a general distribution in northeastern North America from Maine to the Dakotas, south to Texas and Florida. Included here are *C. diandrus, C. pseudovegetus, C. engelmanii, C. lancastriensis, C. ovularis,* and *C. filiculmis.* The same pattern of distribution with an extension into the tropics and into Europe is found in *C. flavescens, C. esculentus,* and *C. densicaespitosus. C. filicinus* is known from the eastern seaboard and from an inland Illinois station.

Species with a distribution throughout continental United States are *C. erythrorhizos, C. ferruginescens,* and *C. strigosus.* An extension of this pattern into Mexico and South America is the distribution of *C. rivularis* and *C. aristatus.*

The remaining four species show a more limited distribution. *Cyperus acuminatus* basically is a western species ranging eastward to Indiana. *Cyperus schweinitzii* and *C. houghtonii* are northern species which include northern Illinois as a southern limit to their ranges. *Cyperus grayioides* is an endemic of the sandy regions of the Illinois River in Mason and Whiteside Counties.

In Illinois, *C. strigosus, C. erythrorhizos, C. esculentus,* and *C. ferruginescens* are common throughout the entire state, frequently becoming weedy. *Cyperus acuminatus* and *C. aristatus* are found sparingly throughout Illinois.

Cyperus pseudovegetus and *C. densicaespitosus* have limited ranges in the southern counties. The former has been recorded only from a few stations north to Wayne County while the latter is known only as far north as Jackson County.

Cyperus ovularis and *C. flavescens* have nearly identical ranges in Illinois, although the latter is much rarer. Both occur in the extreme southern counties with one station recorded from Peoria County. It is probable that neither occur any longer in Peoria County where they have not been found since Brendel's collections during the latter half of the nineteenth century.

Cyperus rivularis is mostly northern in its Illinois distribution, although it is known from St. Clair and Pope Counties. *Cyperus diandrus* is localized in a few northern counties, mostly those bordering the Illinois River, and in Jackson County along the Mississippi River.

Cyperus schweinitzii is found in counties of the northern one-third of Illinois, but is also adventive along a railroad in Jackson County. *Cyperus filiculmis* var. *filiculmis* has a natural range in Illinois similar to *C. schweinitzii*. *Cyperus filiculmis* var. *macilentus* is more widespread, although it is uncommon in the southern counties.

The remaining five species are very rare in Illinois: *Cyperus lancastriensis* from two extreme southern counties (Pulaski and Massac); *C. filicinus* from a roadside ditch in Jackson County where it is possibly adventive; *C. engelmannii* with a disjunct range which includes Lake, McHenry, St. Clair, Union, and Alexander counties; *C. houghtonii* from a railroad in Cook County, and the endemic *C. grayioides* from Mason and Whiteside counties.

ECOLOGICAL CONSIDERATIONS

The Illinois species of *Cyperus* fall into three basic habitat types — sand, low moist ground along bodies of water, and dry fields and bluffs.

Those species which occupy the river banks are subject to frequent inundations which seem to affect their morphology. Many dwarfed and out-of-season specimens are encountered in this habitat.

Cyperus aristatus appears to have the greatest range of tolerance. It is most abundant in low ground, although it is not uncommon in moist depressions atop sandstone bluffs in the southern counties.

Several species reach weedy proportions. *Cyperus esculentus* is very abundant in cultivated fields while *C. strigosus* is a common inhabitant of deserted fields. Even *C. densicaespitosus* is growing rampant in a lawn in Carbondale (Jackson County).

SYSTEMATIC TREATMENT

CYPERUS L. Sp. Pl. ed. 1:44. 1753.

Eucyperus Rikli *in* Pringsheims Jahrb. 27:568. 1895.
Pycreus P. Beauv. Fl. Oware. 2:48. 1807.
Mariscus Gaertn. De Fruct. et Semin. 1:12. 1788.
Kyllinga Rottb. Descr. et Icon. 12. 1773.
Torulinium Desv. *in* Ham., Prodr. Pl. Ind. Occ. 15. 1825.

NATURAL KEY TO THE ILLINOIS SPECIES OF CYPERUS

A. Rhachilla of spikelets continuous; scales gradually deciduous from base of rhachilla to apex.
  B. Stigmas 3; achene trigonous .... Subgenus I. *Cyperus*
  B. Stigmas 2; achene lenticular, compressed to biconvex .... Subgenus II. *Pycreus*
A. Rhachilla of spikelets articulated; scales persistent and then falling all at once from the rhachilla.
  C. Rhachilla not separating into joints.
    D. Stigmas 3; achene trigonous .... Subgenus III. *Mariscus*
    D. Stigmas 2; achene lenticular .... Subgenus IV. *Kyllinga*
  C. Rhachilla articulate at base of each scale .... Subgenus V. *Torulinium*

SUBGENUS I. *Cyperus.*

A. Spikelets disposed on an elongated rhachis.
  B. Spikes cylindric; wings of the rhachilla colored. (Section *Fastigiati*) .... 1. *C. erythrorhizos*
  B. Spikes ovate to broadly turbinate; wings of the rhachilla hyaline. (Section *Esculenti*) .... 2. *C. esculentus*
A. Spikelets on a very short rhachis. (Section *Luzuloidei*).
  C. Perennial; achene linear-oblong .... 3. *C. pseudovegetus*
  C. Annual; achene ellipsoid .... 4. *C. acuminatus*

SUBGENUS II. *Pycreus.*

A. External cells of the achene of isodiametric hexagons.
  B. Scales scarcely sulcate. (Section *Polystachyi*) .... 5. *C. filicinus*
  B. Scales strongly sulcate. (Section *Sulcati*).
    C. Styles cleft nearly to the middle .... 6. *C. rivularis*
    C. Styles cleft nearly to the base .... 7. *C. diandrus*
A. External cells of the achene rectangular-oblong (Section *Flavescentes*) .... 8. *C. flavescens*

SUBGENUS III. *Mariscus.*

A. Spikelets flat or compressed.
  B. Achene linear-oblong. (Section *Strigosi*) .... 9. *C. strigosus*
  B. Achene elliptic-oblong to oblong-ovate.
    C. Plants annual; stamens 1 or 2. (Section *Aristati*) .... 10. *C. aristatus*
    C. Plants perennial; stamens 3. (Section *Laxiglumi*).
      D. All the spikelets ascending .... 11. *C. schweinitzii*
      D. Spikelets divergent.
        E. Spikes ovate; achene as broad as long .... 12. *C. houghtonii*
        E. Spikes globose or hemispherical; achene longer than broad.
          F. Spikes hemispherical; scales mostly acute, approximate .... 13. *C. filiculmis*
          F. Spikes globose; scales obtuse, spreading .... 14. *C. grayioides*
A. Spikelets subterete. (*Section Umbellati*).
  G. Spikelets reflexed in an obovoid head .... 15. *C. lancastriensis*
  G. Spikelets radiating in all directions in a globose head .... 16. *C. ovularis*

SUBGENUS IV. *Kyllinga.*

17. *Cyperus densicaespitosus* of Section *Kyllinga* is our only representative.

SUBGENUS V. *Torulinium.*

Our only representatives belong to Section *Feraces.*

A. Scales approximate, overlapping ....18. *C. ferruginescens*

A. Scales remote, the tip of one barely reaching the base of the one above it ....19. *C. engelmannii*

ARTIFICIAL KEY TO THE ILLINOIS SPECIES OF CYPERUS

A. Achenes lenticular; stigmas 2.
  B. Spikelets 1-flowered; inflorescence of 1-3 sessile heads; plants with a strong sweet odor ....17. *C. densicaespitosus*
  B. Spikelets 5- to 35-flowered; inflorescence of 1-several radiating sessile spikelets and usually 1-several rays; plants essentially inodorous.
    C. Achenes black, nearly as broad as long, with transverse wrinkles; scales stramineous ....8. *C. flavescens*
    C. Achenes drab or gray, longer than broad, without transverse wrinkles; scales usually suffused with purple.
      D. Styles cleft nearly to base, persistent and conspicuously exserted to 4 mm from scales ....7. *C. diandrus*
      D. Styles cleft to about middle, early deciduous, included or projecting to 2 mm from scales.
        E. Scales closely imbricate, strongly suffused with purple (scales stramineous in *C. rivularis* f. *elutus*) ....6. *C. rivularis*
        E. Scales with tips somewhat spreading, the spikelets appearing serrate, stramineous or purple only on the margins ......5. *C. filicinus*

A. Achenes trigonous; stigmas 3.
  F. Scales with strongly reflexed acuminate tips ....10. *C. aristatus*
  F. Scales with tips either appressed or slightly spreading.
    G. Spikes spherical or globose, with spikelets radiating in all directions.
      H. Scales appressed but with the tips shortly excurved; spikes to 8 mm across.
        I. Perennial; achene narrowly lanceolate to linear ....3. *C. pseudovegetus*
        I. Annual achene oblong ....4. *C. acuminatus*
      H. Scales appressed to spreading, their tips straight; some of the heads over 1 cm across.
        J. Scales appressed; spikelets 2- to 3-flowered ....16. *C. ovularis*
        J. Scales spreading; spikelets 5- to several-flowered ......14. *C. grayioides*
    G. Spikes hemispherical, cylindrical, ellipsoidal, or lanceolate, but not globose or spherical.
      K. Spikelets arising from a central axis.
        L. Scales with a mucro 0.5-1.5 mm long; achenes 2.2-3.3 mm long ....11. *C. schweinitzii*
        L. Scales merely acute or with a mucro to 0.5 mm long; achenes usually 1.2-2.1 mm long.
          M. Achenes 1.2-1.5 mm long, 1.2-1.5 mm broad; spikelets nearly all ascending ....12. *C. houghtonii*
          M. Achenes 1.2-2.1 mm long, 0.8-1.1 mm broad; some of the spikelets spreading or slightly reflexed ....13. *C. filiculmis*
      K. Spikelets produced pinnately along the axis.
        N. Scales 1.0-1.5 mm long; achene 0.8-1.0 mm long ....1. *C. erythrorhizos*

N. Scales 1.5-4.5 mm long; achene 1.0-2.8 mm long.
O. Scales very remote, the tip of one just reaching the base of the one above it, giving the spikelet a zigzag appearance ....19. *C. engelmannii*
O. Scales approximate and overlapping.
P. Some or all of the mature spikelets reflexed; spikelets subterete ....15. *C. lancastriensis*
P. None of the spikelets (except sometimes the lowest pair) reflexed; spikelets flattened.
Q. Rhizomes scaly and usually ending in a tuber; scales at the tips of the spikelets rather blunt, giving the spikelet an obtuse appearance ....2. *C. esculentus*
Q. Rhizomes absent or merely becoming hard and corm-like.
R. Plants annual; scales ferruginous or golden-brown; achenes obovoid-oblong, 1.0-1.7 mm long ....18. *C. ferruginescens*
R. Plants perennial; scales stramineous; achenes linear, 1.3-2.2 mm long ....9. *C. strigosus*

1. CYPERUS ERYTHRORHIZOS Muehlenb. Descr. Gram. 20. 1817. (Fig. 1).
Cyperus halei Torr. ex Britt. *in* Bull. Torrey Club 13:213. 1886.
Cyperus erythrorhizos var. *halei* (Torr.) Kükenth in Kükenth., Pflanzenr. 20:59. 1936.

Annual from fibrous, often red, roots; culms to 1.3 meters tall, occasionally dwarfed to 1 cm tall, smooth; leaves to 10 mm wide, shorter than to equalling the culm, with scabrous margins and with the lower sheaths usually purplish near the base; inflorescence of 1-several sessile spikes and numerous simple or compound rays, with up to 8 involucral bracts, most of which surpass the inflorescence; spikes cylindric with numerous horizontally spreading or ascending spikelets; spikelets falcate, 6- to 36-flowered, 3-20 mm long, with closely imbricated scales; scales reddish-brown with stramineous margins, rarely stramineous throughout, with a green midrib, broadly lanceolate, mucronate, faintly nerved, 1.0-1.5 mm long; stamens 2 or 3; styles 3; rhachilla winged; achene trigonous, ovoid, gray or whitish, 0.8-1.0 mm long, about 0.5 mm wide.

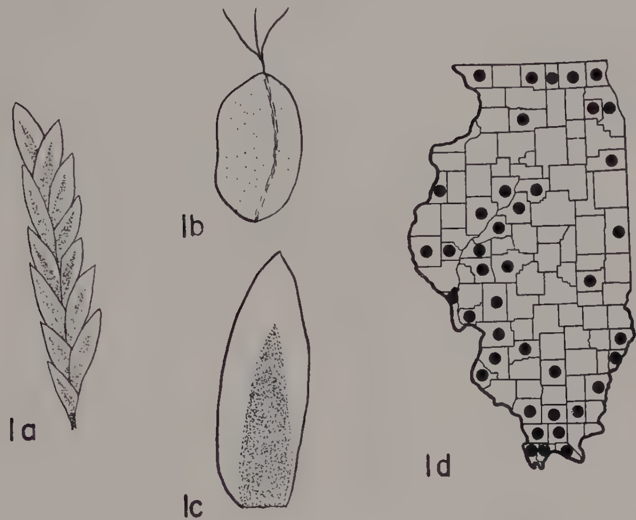
Habitat.—Moist, often sandy soil.

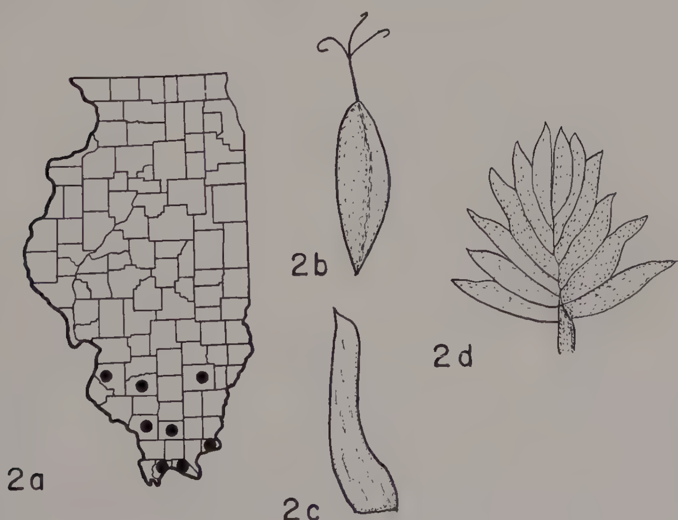
Range.—Massachusetts to Washington south to California and Florida.

Cyperus erythrorhizos is readily distinguished by its tiny reddish-brown scales and gray or whitish achenes which are 0.8-1.0 mm long.

Great variation occurs within the species. Some specimens from Jackson County (*Mohlenbrock 10010*) measured 1.3 meters tall and bore so great an inflorescence that the entire plants toppled to the ground. Specimens as small as 1 cm may be found along river banks which are inundated frequently.

Specimens over 8 dm tall and with spikelets 3-5 mm long have been referred to *Cyperus halei* (or *C. erythrorhizos* var. *halei*), but complete intergradation among entities makes it impossible to main-





Figs. 1 and 2. 1.—*Cyperus erythrorhizos*. a. Spikelet, x 5. b. Achene, x 20. c. Scale, x 30. d. Map. 2.—*Cyperus pseudovegetus*. a. Map. b. Achene, x 20. c. Scale, x 15. d. Spikelet, x 5.

tain *halei* either as a species or a variety. *Ahles 6975* from Pulaski County is only 8 cm tall and bears spikelets 3-5 mm long, but is merely a dwarfed, suppressed form.

Whiting 1802 and *Miller s.n.* are specimens with the scales entirely stramineous.

Specimens Examined: ADAMS: Goose Lake N. of Quincy, *Evers* 15168 (ILLS). ALEXANDER: T17S, R16W, sect. 8, *Evers* 32828 (ILLS). BOONE: W. of Belvidere, *Fell* 541210 (ISM). BROWN: E. of Cooperstown, *Evers* 40562 (ILLS). CALHOUN: N. of Hardin, *Evers* 20420 (ILLS). CASS: One mile S. of Beardstown, *Evers s.n.* (ILLS). CLINTON: SE. of Germantown, *Evers* 20599 (ILLS). COLES: Lake Mattoon, *Stover s.n.* (EI). COOK: N. of Harvey, *Winterringer* 1593 (ILL). DUPAGE: Wheaton, *Fuller* 1949 (ISM). FULTON: Nine miles SE. of Canton, *Miller s.n.* (ILLS). HENDERSON: Oquawka, *Patterson s.n.* (SIU). JACKSON: Near Grand Tower, *Collins s.n.* (SIU). JEFFERSON: E. of Waltonville, *Evers* 52307 (ILLS). JERSEY: Pere Marquette State Park, *Fuller* 541 (ISM). JO DAVIESS: SE. of East Dubuque, *Evers* 49241 (ILLS). JOHNSON: E. of Grantsburg, *Evers* 36015 (ILLS). KANE: Elgin, *Benke s.n.* (F). KANKAKEE: Kankakee, *Hill s.n.* (ILL). LAKE: Two miles NE. of Barrington, *Bennett s.n.* (ILLS). LAWRENCE: SE. of Lawrenceville, *Winterringer* 13492 (ISM). LEE: SE. of Amboy, *Evers* 41003 (ILLS). MCHENRY: Ringwood, *Vasey, s.n.* (ILL). MACOUPIN: Macoupin, *Robertson* 9236 (ILLS). MADISON: E. of Madison, *Evers* 8050 (ILLS). MASON: Swamp, *Rexroat* 1207 (ISM). MASSAC: Near University of Illinois camp, *Fuller* 1802 (SIU). MENARD: Athens, *Hall s.n.* (F). MONROE: S. of Fults, T4S, R10W, *Bailey & Swayne* 2806 (SIU). MORGAN: NE. of Meredosia, *Rexroat* 2195 (ISM). PEORIA: Illinois River, *McDonald* 61½ (ILL). PULASKI: N. of Grand Chain, *Ahles* 6975 (ILL). ST. CLAIR: Fish Lake, *Eggert s.n.* (MO). SALINE: N. of Mitchellsville, *Winterringer s.n.* (ISM). SANGAMON: Clear Lake, *Fuller* 9597 (ISM). TAZEWELL: Near East Peoria, *V. Chase* 3301 (ILL). UNION: Pine Hills swamp, *Stieglitz s.n.* (SIU). VERMILION: Near Danville, *Bock & V. Chase* 2301 (ILL). WABASH: Mt. Carmel, *Schneck* 60 (ILL). WHITE: S. of Mill Shoals, *Ahles* 6635 (ILL). WILLIAMSON: Crab Orchard Lake, *Fuller* 2404 (ISM). WINNEBAGO: Rockford, *Fell* F48-393 (ISM). WOODFORD: Along Illinois River, *V. Chase* 21440 (ILL).

2. CYPERUS ESCULENTUS L. Sp. Pl. 45. 1753.

Perennial from numerous conspicuously scaly rhizomes terminating in a small hard tuber; culms rather stout, to one meter tall, smooth; leaves flat, to 10 mm wide; inflorescence with 1-several sessile spikes and 1-10 rays, with 3-10 broad involucral bracts surpassing the inflorescence; spikes mostly cylindric, with numerous horizontally radiating or ascending spikelets; spikelets flattened, 6- to 30-flowered, 6-35 mm long, 1.5-3.0 mm broad; scales loosely imbricate or spreading somewhat, ovate, obtuse to acute or rarely with the terminal scale acuminate, 7- to 11-nerved, 2-3 mm long, stramineous or golden brown, scarious at the tip; rhachilla winged; achenes oblongoid to narrowly oblongoid, 1.2-1.8 mm long, 0.4-0.8 mm broad, brownish or grayish.

Habitat.—Moist, frequently cultivated soil.

Range.—Maine to Washington south to Arizona and Florida; Mexico; tropical America; Europe.

Two varieties may be separated as follows:

a. Inflorescence simple to compound; spikelets to 15 mm long, 1.5-3.0 mm broad; scales loosely or usually closely imbricate, obtuse, or the terminal mucronulate; achene obovoid ....*C. esculentus* var. *esculentus*

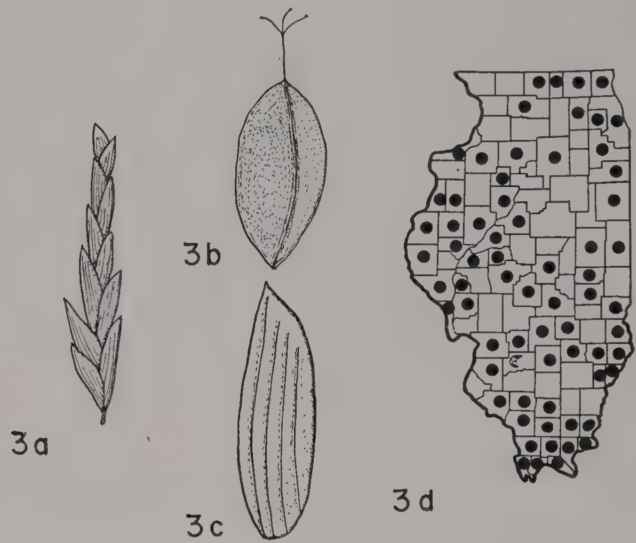
a. Inflorescence compound; spikelets longer and narrower, 20-35 mm long and less than 1.5 mm broad; scales loosely imbricate, mucronulate; achenes narrowly oblongoid ....*C. esculentus* var. *leptostachyus*

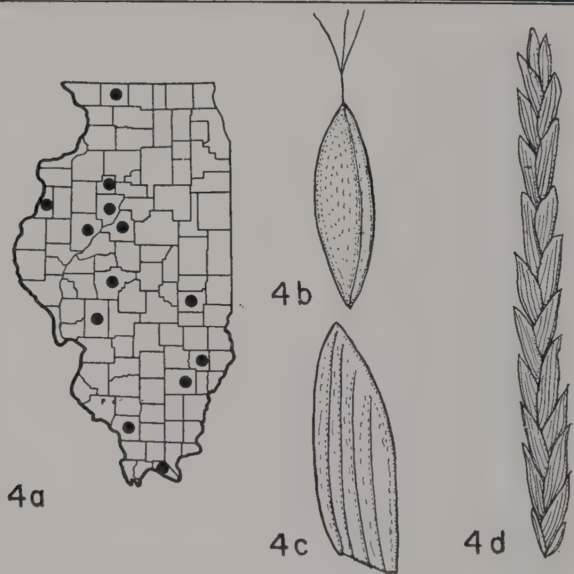
2a. *Cyperus esculentus* var. *esculentus* (Fig. 3).

Cyperus phymatodes Muehlenb. Descr. Gram. 23. 1817 (in part).

The typical variety is a troublesome weed in recently cultivated ground throughout Illinois. The common name of Nut-grass is from the presence of tubers at the ends of the rhizomes. The presence of scales on the rhizomes readily identifies this species.

Specimens Examined: ADAMS: N. of Quincy, *Evers* 15191 (ILLS). ALEXANDER: Three and one-half miles N. of Olive Branch, *Evers* 18693 (ILLS). BOND: SE. of Hookdale, *Evers* 48861 (ILLS). BOONE: Near Caledonia, *Fell* 54952 (ISM). BUREAU: E. of Mineral, *Evers* 21201 (ILLS). CALHOUN: Pere Marquette Wildlife Research Area, *Muller* 9743 (ILLS). CASS: River bank, *Rexroat* 1116 (ISM). CHAMPAIGN: Waste ground, University of Illinois, *Gibbs* 28615 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). CLARK: S. of Marshall, *Evers* 19741 (ILLS). CLAY: Flora, *Amman* 14618 (ILLS). CLINTON: *Evers* 12484 (ILLS). COLES: Humboldt, *Amman* 14620 (ILLS). COOK: River Forest, *Moffatt* 265 (ILL). CRAWFORD: NW. of Hutsonville, *Evers* 19757 (ILLS). DOUGLAS: N. of Arcola, *Winterringer* 3492 (ISM). DUPAGE: Wheaton, *Fuller* 1906 (ISM). EDWARDS: W. of Albion, *Evers* 20174 (ILLS). EFFINGHAM: One mile NE. of Effiingham, *Evers* 5743 (ILLS). FAYETTE: S. of St. Elmo, *O'Dell* 44 (ILL). FRANKLIN: One mile S. of Rand City, *Evers* 52389 (ILLS). FULTON: N. of Lewiston, *Evers* 14913 (ILLS). GALLATIN: ½ mile S. of Ridgway, *G. Dillard s.n.* (SIU). GREENE: SE. of Greenfield, *Evers* 20703 (ILLS). HANCOCK: NW. of Bowen, *Evers* 26981 (ILLS). HARDIN: Elizabethtown, *Evers* 11290 (ILLS). HENDERSON: E. of Shakoken, *Evers* 18343 (ILLS). HENRY: E. of Atkinson, *Evers* 21178 (ILLS). IROQUOIS: E. of Milford, *Ahles* 3158 (ILL). JACKSON: Grand Tower, *Fuller & Fisher* 271 (ISM). JOHNSON: SW. of Forman, *Evers* 19921 (ILLS). KANE: Elgin 3663 (F). KANKAKEE: Six miles W. of Kankakee, DeSelm 413 (F). LAKE: Libertyville, *Mathins s.n.* (ILL). LASALLE: Starved Rock State Park, *Werner* 9797 (ILLS). LAWRENCE: One-half mile E. of Sumner, *Sivert* 107 (ILL). MCDONOUGH: N. of Bushnell, *Myers* 1170 (ISM). MCHENRY: Near Algonquin, *Nason* 20760 (ILL). MACON: Two miles S. of Niantic, *Clokey* 2448 (ILL). MACOUPIN: Carlinville, *Fuller* 2259 (ISM). MADISON: E. of Madison, *Evers* 14097 (ILLS). MARION: Near Patoka, *Winterringer* 3498 (ISM). MASON: Four miles S. of Easton, *Robinson* 12399 (ISM). MASSAC: Brookport, *Fuller & Welch* 348 (ISM). MENARD: Athens, *Hall* 29400 (ILL). OGLE: Rock River, *Moffatt* 460 (ILL). PEORIA: Peoria, *McDonald s.n.* (ILL). PIKE: N. of Florence, *Evers* 20300 (ILLS). POPE: N. of Eddyville, *Mohlenbrock* 10011 (SIU). PULASKI: Douglas Landing, *Evers* 41453 (ILLS). RANDOLPH: Four miles SW. of Prairie du Rocher, *Trojcak* 3084 (ISM). RICHLAND: Four miles N. of Olney, *Shaw* 691 (ISM). ROCK ISLAND: SW. of Hillsdale, *Evers* 21101 (ILLS). ST. CLAIR: Near French Village, *Neill* 913 (ISM). SALINE: Harrisburg, *Stout* 9805 (ILLS). SANGAMON: Clear Lake, *Fuller* 8832 (ISM). SCHUYLER: Two and one-half miles SW. of Beardstown, *Rexroat* 2318 (ISM). SCOTT: Four miles W. of Winchester, *Flynn* 14302 (ISM). SHELBY: Shelby-





Figs. 3 and 4. 3.—*Cyperus esculentus* var. *esculentus*. a. Spikelet, x 4. b. Achene, x 20. c. Scale, x 15. d. Map. 4.—*Cyperus esculentus* var. *leptostachyus*. a. Map. b. Achene, x 15. c. Scale, x 15. d. Spikelet, x 3.

ville, *Fisher s.n.* (EI). STARK: S. of Bradford, *Evers* 21234 (ILLS). TAZEWELL: Mackinaw, *Stillman* 9803 (ILLS). UNION: Wolf Lake, *Fuller & Fisher* 780 (ISM). VERMILION: Between Oakwood and Collison, *G. Jones* 12999 (ILL). WABASH: Near Sportsman's Park, *Schneck s.n.* (ILL). WARREN: W. of Monmouth, *Evers* 20988 (ILLS). WASHINGTON: Five miles W. of Ashley, *Boewe* 14621 (ILLS). WILL: Lockport, *Hill* 3137 (ILL). WILLIAMSON: Crab Orchard Lake, *S. Abney & G. Dillard* 29 (SIU). WINNEBAGO: Rockford, *Fell & Fell* 147-380 (ISM).

2b. *Cyperus esculentus* var. *leptostachyus* Boeckl. Linnaea 36:290. 1870. (Fig. 4).

Cyperus phymatodes Muehlenb. Descr. Gram. 23. 1817.
Cyperus esculentus f. *angustispicatus* (Britt.) Fern. Rhodora 44: 151. 1942.

This variety, with larger and narrower spikelets, has achenes which average longer and narrower than those in var. *esculentus*.

Specimens Examined: COLES: One mile NW. of Oakland, *Voigt* 918 (SIU). FULTON: Canton, *Wolf s.n.* (F). HENDERSON: Oquawka, *Patterson s.n.* (ILL). JACKSON: Fountain Bluff, *Cranwill s.n.* (ILL). MACOUPIN: Carlinville, *Robertson* 9762 (ILLS). MASSAC: Five miles E. of Brookport, *McCree* 348 (SIU). PEORIA: Near Farmington, *V. Chase* 4732 (ILL). RICHLAND: Sugar Creek prairie, *Ridgway* 255 (F). ST. CLAIR: Indian Lake, Eggert *s.n.* (F). SANGAMON: Clear Lake, *Fuller* 6256 (ISM). STARK: Near Wady Petra, *V. Chase* 1542 (ILL). STEPHENSON: Near Redott, *Fell* 52905 (ISM). TAZEWELL: Pekin, *V. Chase* 19858 (ILL). WAYNE: E. of Fairfield, *Walker* 50 (ILL).

3. CYPERUS PSEUDOVEGETUS Steud. Synops. Cyper. 24. 1855. (Fig. 2).

Cyperus virens Gray, Manual ed. 2:493. 1856, non. Michx.

Perennial from a short rhizome; culms 35-65 cm tall, glabrous; leaves 2-4 mm wide, usually equalling the culm, glabrous; inflorescence of 1-several sessile heads and numerous compound rays; spikes with numerous radiating spikelets; spikelets 5- to 13-flowered, 3.0-6.5 mm long, with rather loosely arranged scales; scales narrow, subacute, with slender excurved tips, 1.8-2.2 mm long, faintly-nerved, pale greenish-yellow; stamen 1; style 3-cleft; achenes linear, 1.0-1.4 mm long, stipitate, stramineous.

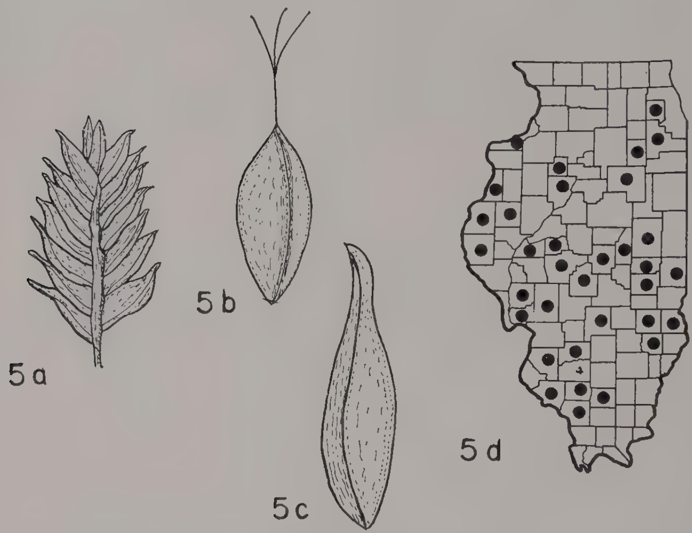
Habitat.—Moist soil.

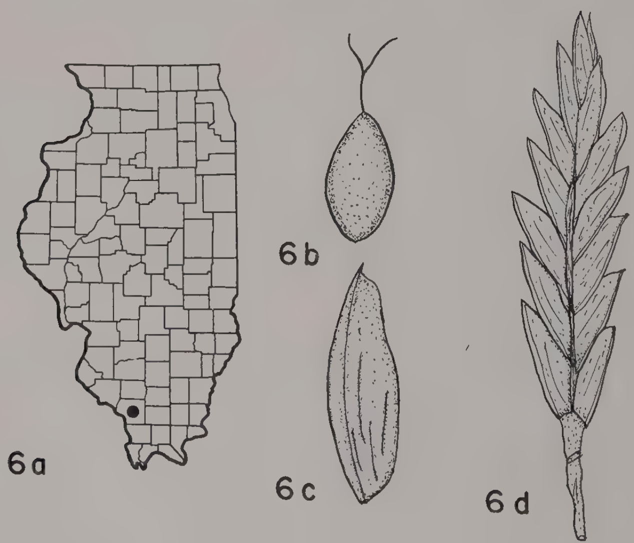
Range.—New Jersey to Kansas south to Texas and Florida.

This sedge is one of the rarer species of *Cyperus* in Illinois. It has been collected in eight counties, all in the southern one-third of the state.

It is related closely to *C. acuminatus* which it resembles strongly. *Cyperus pseudovegetus,* however, is a perennial which grows considerably taller than *C. acuminatus* and also has narrower scales and achenes.

Specimens Examined: JACKSON: Carbondale, *V. H. Chase* 9978 (ILL). MASSAC: Metropolis, *H. C. Benke* 4700 (F). PULASKI: S. of Ullin, *R. A. Evers* 19998 (ILLS). ST. CLAIR: Wet places, *H. Eggert s.n.* (F). WABASH: N. of Mt. Carmel, *W. Bailey & J. R. Swayne s.n.* (SIU) WASHINGTON: Venedy Station, *Evers* 33946 (ILLS). WAYNE: Five miles N. of Cisne, *Winterringer* 3446 (ILLS). WILLIAMSON: Crab Orchard Lake, *Evers* 18629 (ILLS).





Figs. 5 and 6. 5.—*Cyperus acuminatus.* a. Spikelet, x 6. b. Achene, x 25. c. Scale, x 20. d. Map. 6.—*Cyperus filicinus.* a. Map. b. Achene, x 15. c. Scale, x 15. d. Spikelet, x 3.

4. CYPERUS ACUMINATUS Torr. & Hook. Ann. Lyc. N. Y. 3:435. 1836. (Fig. 5).

Cespitose annual with fibrous roots; culms 4-35 cm tall, usually stramineous; leaves few, 1-2 mm wide, nearly equalling or slightly exceeding the culm; involucral bracts 2-4, exceeding the inflorescence, the longest to 8 cm, 1-2 mm wide; inflorescence of numerous spikes 1-2 cm in diameter, borne on rays 1-4 cm long, usually with one or more sessile spikes; spikelets flattened, ovate to oblong, rarely linear, ascending or spreading, closely imbricated, 12- to 40-flowered; scales ovate, acute, outwardly curved at the tip, 1.8-2.6 mm long, pale, with one conspicuous central nerve and usually 2-4 very obscure lateral ones; stamen 1; style cleft; achenes ellipsoid to oblongoid, pointed at either end, 0.5-1.0 mm long, 0.5 mm broad, much surpassed by the scales, stramineous.

Habitat.—Wet ground.

Range.—Indiana to North Dakota south to Texas and Florida; Washington, Oregon.

Cyperus acuminatus resembles *C. aristatus* in its recurved scales, but those of *C. aristatus* are much more recurved. *Cyperus acuminatus* lacks the Slippery Elm aroma so characteristic of *C. aristatus.*

Specimens Examined: ADAMS: Melrose, *Brinker* 3568 (ISM). ALEXANDER: McClure, *Cranwill s.n.* (ILL). CHAMPAIGN: Near Champaign, *Burrill & Seymour* 18574 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). CLINTON: Between Carlyle and Shattuc, *Ahles* 6056 (ILL). COLES: N. of Mattoon, *Stover s.n.* (EI). CRAWFORD: Between Oblong and Stoy, *Ahles* 4946 (ILL). DOUGLAS: Arcola, *Mohr* 9723 (ILLS). DUPAGE: *Hawkins* 9724 (ILLS). EDGAR: W. of Paris, *Evers* 7354 (ILLS). FAYETTE: Near Pecan Island, *O'dell* 591 (ILL). FRANKLIN: N. of Benton, *Ahles* 5532 (ILL). GREENE: N. of Eldred, *Evers* 20324 (ILLS). GRUNDY: SW. of Gardner, *Evers* 21684 (ILLS). HANCOCK: Augusta, *Mead s.n.* (MO). HENDERSON: Near Oquawka, *Patterson s.n.* (ILL). JACKSON: S. of Murphysboro, *Hardy & Voigt* 128 (ISM). JASPER: Newton, *Boewe* 9729 (ILLS). JERSEY: Kemper, *McDonald s.n.* (ILL). LIVINGSTON: SW. of Cayuga, *Evers* 21712 (ILLS). MCDONOUGH: S. of Bushnell, *V. Chase* 11500 (ILL). MACON: Decatur, *Clokey* 1080 (MO). MACOUPIN: One mile S. of Hettick, *Winterringer* 3487 (ISM). MARION: W. of Brubaker, *Evers* 20649 (ILLS). MASON: *Brendel s.n.* (ILL). MENARD: Athens, *Hall s.n.* (MO). PEORIA: "West Bluff," Peoria, *McDonald s.n.* (ILL). PERRY: S. of Pyatts, *Evers* 18725 (ILLS). PIATT: N. of Monticello, *Ahles* 6566 (ILL). RANDOLPH: Between Chester and Evansville, *Ahles* 5666 (ILL). RICHLAND: Three and one-half miles N. of Olney, *Shaw* 729 (ISM). ROCK ISLAND: E. of Cordova, *Evers* 35499 (ILLS). ST. CLAIR: Cahokia, *Neill* 1363 (ISM). SANGAMON: Springfield Township, *Carter* 14370 (ISM). STARK: Near Wady Petra, *V. Chase* 682 (ILL). WASHINGTON: Nashville, *French* 3023 (SIU). WILL: Lockport, *Hill s.n.* (ILL).

5. CYPERUS FILICINUS Vahl, Enum. 2:332. 1806. (Fig. 6).

Annual from fibrous roots; culms to 30 cm tall, smooth; leaves to 3 mm wide, shorter than the culm, smooth; inflorescence of 1-2 sessile heads and 1-3 rays to 6 cm long, with 3-6 involucral bracts, some normally exceeding the inflorescence; spikes with up to 10 spikelets

radiating in all directions; spikelets very flat, linear-lanceolate, acute, 12- to 25-flowered, to 25 mm long, 3 mm broad; scales broadly lanceolate, stramineous or golden brown, acute, mucronulate, 2.0-3.5 mm long; stamens 2; styles deeply 2-cleft; achenes narrowly obovoid, obtuse at summit, 1.2-1.6 mm long, brownish.

Habitat.—Wet, usually brackish soils.

Range.—Maine to Florida and Louisiana; West Indies.

The discovery of this east coast sedge in a roadside ditch in southern Illinois in 1950 has come as a complete surprise. Because of the roadside habitat, it would appear to be adventive except that all its associates at this station (*Carex lanuginosa, Juncus tenuis*, etc.) are part of the native wet ditch flora of southern Illinois.

Specimen Examined: JACKSON: Roadside ditch along Highway 51, N. of DeSoto, *Voigt* 391 (SIU).

6. Cyperus rivularis Kunth, Enum. 2:6: 1837. (Fig. 7).

Annual from fibrous roots; culms to 50 cm tall, smooth; leaves to 3 mm broad, nearly equalling the culm, smooth; inflorescence of 1 or 2 sessile heads and usually with 1-5 rays to 8 cm long, with 3 (-4) involucral bracts much exceeding the inflorescence; spikes with up to 10 spikelets radiating in all directions; spikelets very flat, blunt, 8- to 35-flowered, to 25 mm long and 4 mm broad; scales closely imbricated, ovate, obtuse, 2.0-2.5 mm long, strongly colored red-brown from near the mid-vein to the margins, or rarely merely stramineous; stamens 2 or rarely 3; styles 2-cleft to about the middle, early deciduous; achenes narrowly obovate, 1.0-1.5 mm long, 0.5-0.8 mm broad, chestnut or grayish.

Habitat.—Wet ground along banks and shores.

Range.—Maine to South Dakota south to Texas and Georgia; California; Mexico.

Three forms recognizable in Illinois may be separated as follows:

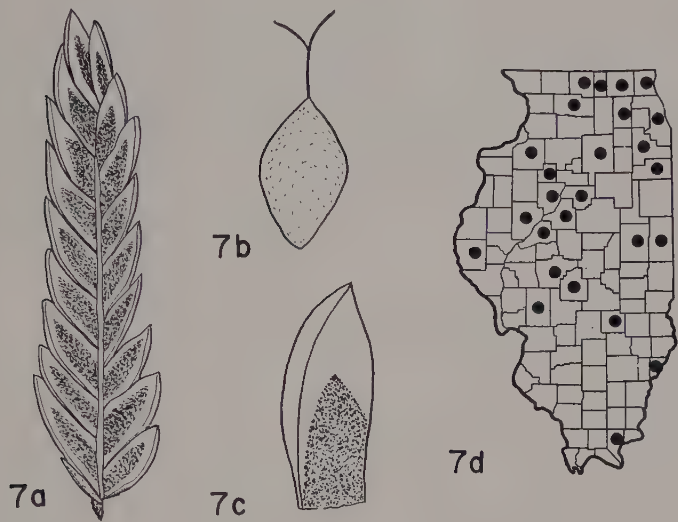
a. Scales strongly suffused with red-brown or purple pigmentation.
  b. Culms to 30 cm tall .... *C. rivularis* f. *rivularis*
  b. Culms (30-) 40-50 cm tall .... *C. rivularis* f. *elongatus*
a. Scales stramineous throughout, except for the greenish midrib .... *C. rivularis* f. *elutus*

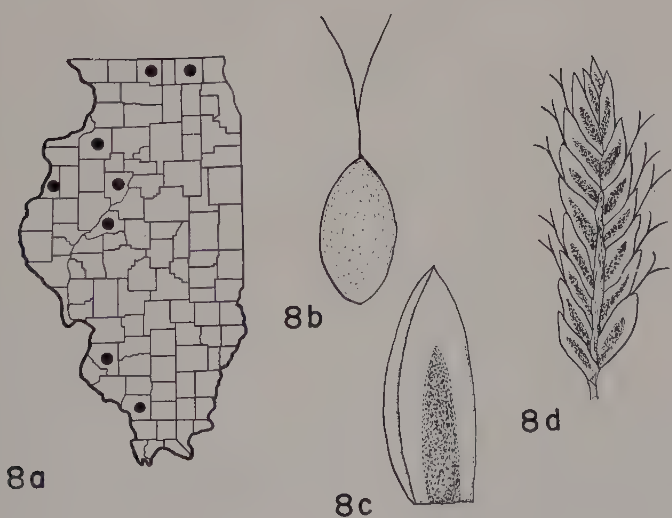
6a. *Cyperus rivularis* f. *rivularis*

Cyperus diandrus Torr. var. *castaneus* Torr. *in* Ann. Lyc. N.Y. 3:252. 1836.

The typical form is rather abundant in northern and central Illinois where it grows along rivers and the edges of ponds and lakes. It is extremely rare in the southern counties.

Specimens Examined: ADAMS: Eight miles SE. of Quincy, *Brinker* 3020 (ISM). BOONE: Kishwaukee River, *E. W. Fell* 52783 (ISM). CHAMPAIGN: Urbana, *Clinton* 28612 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). COOK: Grand Crossing, Chicago, *A. Chase* 2004 (ILL). EFFINGHAM: Nine miles S. of Effingham, *Winterringer* 8994 (ISM). FULTON: *Clinton* 28737





Figs. 7 and 8. 7.—*Cyperus rivularis*. a. Spikelet, x 3. b. Achene, x 20. c. Scale, x 15. d. Map. 8.—*Cyperus diandrus*. a. Map. b. Achene, x 15. c. Scale, x 15. d. Spikelet, x 2.

(ILL). HENRY: Near Colma, *E. W. Fell & G. B. Fell* 46833 (ISM). KANE: Trout Park, Elgin, *Fuller* 9299 (ISM). KANKAKEE: St. Anne, *Graham* 1907 (ISM). LAKE: Illinois Beach State Park, *Winterringer* 8975 (ISM). LASALLE: Starved Rock State Park, *Ries* 7547 (ISM). MCHENRY: Three miles NW. of Ringwood, *Fuller* 13311 (ISM). MACOUPIN: Carlinville, *Robertson* 9731 (ILLS). MASON: Havana, *Fuller* 1839 (ISM). OGLE: Rock River, *Moffatt* 459 (ILL). PEORIA: Near Peoria, *Brendel s.n.* (ILL). POPE: Lake Glendale, *Bailey & Swayne* 3017 (ISM). SANGAMON: Salisbury, *Fuller* 7941 (ISM). STARK: *V. Chase s.n.* (ILL). TAZEWELL: Near Spring Mills, *V. Chase* 3314 (ISM). VERMILION: Kickapoo State Park, *Ahles* 1782 (ISM). WABASH: Near Patton, *Schneck s.n.* (ILL). WILL: Braidwood, *Graham* 9938 (ISM). WINNEBAGO: Rockford, *Fuller s.n.* (ISM). WOODFORD: Spring Bay, *V. Chase* 10100 (ILL).

6b. *Cyperus rivularis* f. *elongatus* Boeckl. *in* Linnaea 35:453. 1868 (pro. var.).

The tall form which at maturity may reach a height of 50 cm, has a very strikingly slender appearance. It is rare in Illinois where it grows with the typical form.

Specimens Examined: COLES: Three miles E. of Charleston, *Stover s.n.* (EI). TAZEWELL: Near East Peoria, Spring Mill Bay, *V. Chase* 9042 (ILL).

6c. *Cyperus rivularis* f. *elutus* C. B. Clarke *in* Journ. Linn. Soc. 21:65. 1884.

This form curiously resembles *Cyperus flavescens* because of the lack of red-brown pigmentation of the scales. However, the achenes of f. *elutus* are usually 1.2-1.5 mm long and narrowly obovate while those of *C. flavescens* are about 1 mm long and broadly obovate.

Specimens Examined: COLES: Three miles E. of Charleston, *Stover* 437-A (EI). WABASH: Mt. Carmel, *Schneck s.n.* (ILL).

7. CYPERUS DIANDRUS Torr. Cat. Pl. N. Y. 90. 1819. (Fig. 8).

Annual from fibrous roots; culms to 40 cm tall, smooth; leaves to 3 mm wide, nearly equalling the culm, smooth; inflorescence of 1 or 2 sessile heads and usually 1-5 rays to 6 cm long, with 3 involucral bracts exceeding the inflorescence; spikes with up to 10 spikelets radiating in all directions; spikelets very flat, blunt, 5- to 35-flowered, to 25 mm long and 4 mm broad; scales closely imbricated, ovate, 2-3 mm long, obtuse, with a reddish-purple band along the margins which sometimes extends to near the midrib; stamens 2 or rarely 3; styles 2-cleft nearly to the base, protruding to 4 mm from the tips of the scales, persistent; achene narrowly obovoid, 1.0-1.5 mm long, somewhat more than half as broad.

Habitat.—Wet ground along banks and shores.

Range.—New Brunswick to North Dakota south to New Mexico and South Carolina.

Much confusion exists in the separation of *C. diandrus* from *C. rivularis.* Many Illinois specimens called *C. diandrus* are actually *C.*

rivularis, a fact which greatly restricts the known range of *C. diandrus* in Illinois.

Separation based on the red-brown pigmentation of the scales is not too reliable. Whether the style is cleft to the middle, or to the base, is difficult to determine frequently due to the fragility of the styles. The most easily observed difference is that the styles of *C. diandrus* project to 4 mm from the scales and are persistent; the styles of *C. rivularis* are included within the scales or project to only 2 mm and are rarely deciduous.

C. diandrus is known in Illinois from a few stations mostly in the northern counties.

Specimens Examined: HENDERSON: Oquawka, *Patterson s.n.* (F). HENRY: N. side of Penny Slough, *Dobbs* 19498 (ILLS). JACKSON: Along Mississippi River near Grand Tower, *S. Abney & G. Dillard* 270 (SIU). MCHENRY: Algonquin, *Nason s.n.* (ILL). MASON: *Ahles* 29403 (ILL). PEORIA: Peoria, *Brendel s.n.* (ILL). ST. CLAIR: Bank of the Mississippi River, *H. Eggert s.n.* (MO). WINNEBAGO: Rockford, *E. W. Fell s.n.* (ISM).

8. CYPERUS FLAVESCENS L. Sp. Pl. 46. 1753. (Fig. 9).

Cyperus poaeformis Pursh, Fl. Am. Sept. 1:50. 1814.
Cyperus flavescens var. *poaeformis* (Pursh) Fern. Rhodora 41:529. 1939.

Cespitose annual; roots fibrous; culms 8-45 cm tall, straw-colored, rarely becoming purplish near the base, smooth, 0.5-1.5 mm broad; leaves 0.5-2.0 mm wide, about one-half to two-thirds as long as the culms; bracts usually 3, rarely 2-4, at least one and sometimes all of them exceeding the inflorescence, the longest to 12 cm, 0.5-2.0 (rarely to 3.0) mm broad; spikes crowded into condensed umbels or occasionally with 1-3 rays up to 3cm long; spikelets very flat, 12- to 25-flowered, 5-15 mm long, 2.0-3.0 mm broad, obtuse at the tip; scales pale yellowish-brown, ovate, obtuse, with broad hyaline margins, distinctly green-keeled, 1.5-2.5 mm long; stamens 3; styles deeply 2-cleft; achene flattened, obovate, with minute transverse wrinkles, 0.8-1.0 mm long, nearly as broad, apiculate, black.

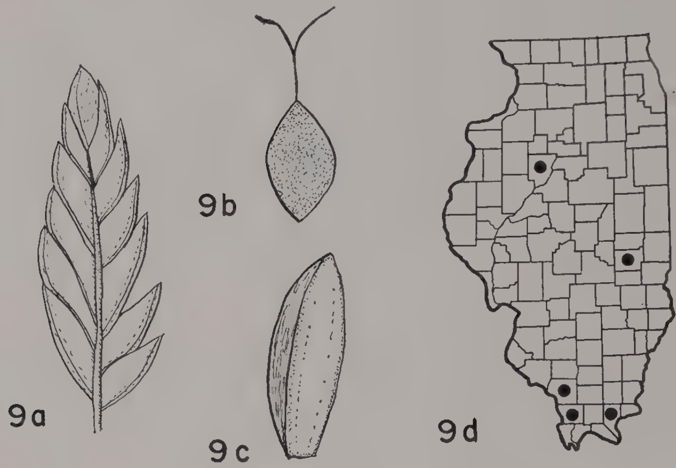
Habitat.—Wet open soil.

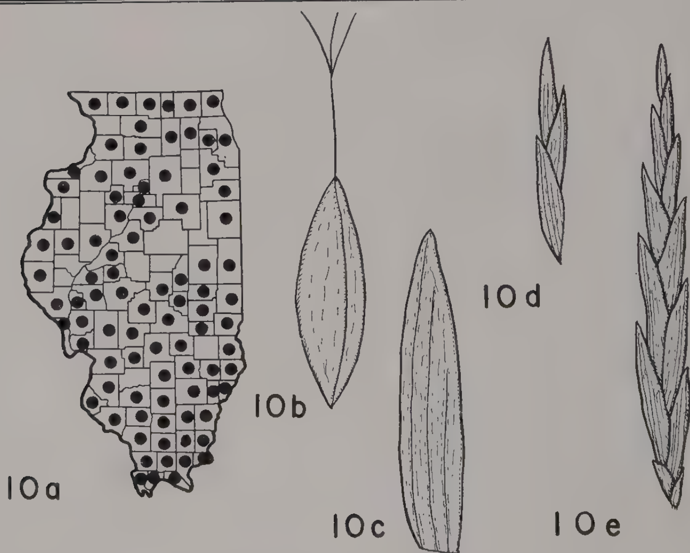
Range.—Massachusetts to Michigan south to Texas and Florida; tropical America; Europe.

A comparative study of *Cyperus flavescens* from the Old World with North American material reveals no reason to consider the New World specimens varietally distinct. *Montpellier* 3957 from Pyranée, France, for example, is totally indistinguishable from United States material.

Cyperus flavescens is exceedingly rare in Illinois. It is most common in the extreme southern counties, although there is a collection of it from Peoria County. This species very closely resembles *C. rivularis* f. *elutus,* but may be distinguished on the basis of the achene.

Specimens Examined: COLES: Rock Park, *Stover s.n.* (EI). JACKSON: Mid-





Figs. 9 and 10. 9.—*Cyperus flavescens*. a. Spikelet, x 4. b. Achene, x 15. c. Scale, x 15. d. Map. 10.—*Cyperus strigosus*. a. Map. b. Achene, x 15. c. Scale, x 10. d-e. Spikelets, x 4.

land Hills Country Club, *Voigt* 2928 (SIU). PEORIA: Peoria, *Brendel s.n.* (ILL). POPE: Lake Glendale, *Bailey & Swayne* 3016 (SIU). UNION: Cobden, collector unknown.

9. CYPERUS STRIGOSUS L. Sp. Pl. 47. 1753. (Fig. 10).

Cyperus stenolepis Torr. Ann. Lyc. N.Y. 3:263. 1836.
Cyperus strigosus f. *robustior* Kunth, Enum. 2:88. 1837.
Cyperus strigosus var. *robustior* (Kunth) Britt. Bull. Torr. Club 13:212. 1886.
Cyperus strigosus var. *stenolepis* (Torr.) Kükenth. *in* Fedde, Rep. 23:189. 1926.

Perennial from a hard corm-like rhizome; culms to 1.2 m tall, smooth; leaves flat, to 12 mm wide, some of them surpassing the culms; inflorescence with 1-2 sessile heads and 2-12 simple or compound rays, with several of the numerous bracts much longer than the inflorescence; spikes cylindric, with numerous horizontally radiating or ascending spikelets; spikelets strongly flattened, 3- to 25-flowered, to 30 mm long, with appressed or loosely ascending scales; scales acute and often mucronulate, 3.5-5.0 mm long, 7- to 11-nerved, golden-brown, with scarious margins; rhachilla winged; achene linear to linear-oblongoid, 1.3-2.2 mm long, 0.4-0.7 mm broad.

Habitat.—Wet ground.

Range.—Quebec to South Dakota south to Texas and Florida; west coast of the United States.

Cyperus strigosus is one of our most variable species with every degree of intergradation occurring among several characters. Very robust specimens with appressed scales (f. *robustior*) or loosely arranged scales (var. *stenolepis*) occur, but intergradations of all degrees may be found from the smallest to the largest variations. It does not seem feasible to retain any of the named variations.

Cyperus strigosus occurs in very moist soil probably in every county of Illinois.

Specimens Examined: ADAMS: Three miles E. of Ursa, *Brinker* 2964 (ILL). ALEXANDER: N. of Tamms, *Evers* 15506 (ILLS). BOND: S. of Greenville, *Winterringer* 12982 (ISM). BOONE: W. of Belvedere, *E. W. Fell* 54897 (ISM). BUREAU: E. of Mineral, *Evers* 21199 (ILLS). CALHOUN: NW. of Belleview, *Evers* 41243 (ILLS). CASS: Eight miles SW. of Beardstown, *Winterringer* 5247 (ISM). CHAMPAIGN: Mahomet, *Seymour* 18593 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (II). CLARK: S. of Marshall, *Winterringer* 7041 (ISM). CLAY: Clay City, *Ahles s.n.* (ILL). CLINTON: N. of Beckemeyer, *Evers* 14303 (ILLS). COLES: E. of Charleston, *Stover s.n.* (EI). CRAWFORD: NW. of Hutsonville, *Evers* 19758 (ILLS). CUMBERLAND: SW. of Casey, collector unknown, (ILLS). DEKALB: Kingston, *Evers* 19121 (ILLS). DOUGLAS: Near Tuscola, *Fuller* 12046 (ISM). DUPAGE: Wheaton, *Fuller* 1906 (ILLS). EDGAR: W. of Paris, *Evers* 7353 (ILLS). EDWARDS: Five miles S. of Albion, *Evers* 31637 (SIU). EFFINGHAM: SE. of Watson, *Evers* 48200 (ILLS). FAYETTE: Two miles SE. of Ramsey, *Fuller* 14000 (ISM). FRANKLIN: S. of Logan, *Evers* 41383 (ILLS). FULTON: Canton, collector unknown, (ILL). GALLATIN: Three miles N. of Omaha, *Evers* 19899 (ILLS). GREENE: W. of Carrollton, *Winterringer* 13030 (ISM). HAMILTON: E. of Piopolis, *Evers* 13136

(ILLS). HANCOCK: Carthage, *Gates* 10002 (ILL). HARDIN: E. of Karber's Ridge, *Evers* 8516 (ILLS). HENDERSON: Crystal Lake, *Hawkins* 9801 (ILLS). HENRY: Seven miles N. of Geneseo, *Evers* 35512 (ILLS). IROQUOIS: sandy region, *Tehon* 9806 (ILLS). JACKSON: Giant City State Park, *Mohlenbrock s.n.* (SIU) JEFFERSON: S. of Mt. Vernon, *Ahles* 5492 (ILL). JERSEY: Pere Marquette State Park, *Fuller* 2030 (ISM). JO DAVIESS: S. of Blanding, *Evers* 35756 (ILLS). JOHNSON: E. of Vienna, *Winterringer* 7042 (ISM). KANE: Elgin, *Sherff* 1806 (ILL). KANKAKEE: Kankakee, *Schultes s.n.* (ILL). LAKE: East Zion, *Brown* 117 (ILL). LASALLE: Starved Rock State Park, *Ries* 7546 (ISM). LAWRENCE: SW. of Birds, *Evers* 19793 (ILLS). LEE: Two miles E. of Kingdom, *Keithley* 293 (ISM). LIVINGSTON: SW. of Cayuga, *Evers* 21693 (ILLS). MCDONOUGH: S. of Bushnell, *V. Chase* 11506 (ILL). MCHENRY: Algonquin, *Nason s.n.* (ILL). MACON: Lake Decatur, *Winterringer* 6534 (ISM). MACOUPIN: N. of Bunker Hill, *Winterringer* 12987 (ISM). MADISON: Near Livingston, *Winterringer* 13168 (ISM). MARION: Near Patoka, *Winterringer s.n.* (ISM). MARSHALL: S. of Lacon, *Evers* 19598 (ILLS). MASON: Havana, *Fuller* 1836 (ISM). MASSAC: E. of Joppa, *Evers* 36485 (ILLS). MENARD: Three miles E. of Oakford, *Evers* 12990 (ILLS). MONROE: SE. of Poe, *Evers* 20505 (ILLS). MONTGOMERY: S. of Litchfield, *Evers* 14060 (ILLS). MORGAN: Three miles NE. of Meredosia, *Rexroat* 2061 (ISM). MOULTRIE: NW. of Sullivan, *Winterringer* 9156 (ISM). OGLE: Four miles E. of Oregon, *Fuller* 9277 (ISM). PEORIA: Peoria, *McDonald s.n.* (ILL). PERRY: One mile S. of Tamaroa, *Winterringer* 9421 (ISM). PIATT: Monticello, *G. Jones* 18912 (ILL). PIKE: N. of Florence, *Evers* 20309 (ILLS). POPE: Belle Smith Springs, *Evers* 52607 (ILLS). PULASKI: N. of Pulaski, *Mohlenbrock & Voigt* 5549 (SIU). PUTNAM: Lake Senachwine, *V. Chase* 10801 (ILL). RANDOLPH: One and one-half miles N. of Prairie du Rocher, *Trojcak* 3162 (ISM). RICHLAND: Lower Wabash valley, *Ridgway* 1212 (ILL). ROCK ISLAND: S. of Cordova, *Evers* 13927 (ILLS). ST. CLAIR: N. of Mascoutah, *Evers* 20570 (ILLS). SALINE: Sahara Lake, *S. Abney & G. Dillard* 85 (SIU). SANGAMON: Rochester, *Fuller* 5478 (ISM). SCOTT: Four miles W. of Winchester, *Flynn* 14302 (ISM). SHELBY: SW. of Lakewood, *Evers* 35931 (ILLS). STARK: Wady Petra, *V. Chase* 1208 (ILL). STEPHENSON: Three miles W. of Seward, *E. Fell* 52822 (ISM). TAZEWELL: S. of Pekin, *E. Fell* 5 (ISM). UNION: S. of Jonesboro, *Winterringer* 11998 (ISM). VERMILION: Danville, Kickapoo State Park, *Miller s.n.* (ILL). WABASH: Near Mt. Carmel, *Schneck s.n.* (ILL). WASHINGTON: Irvington, *French s.n.* (SIU). WAYNE: Near Cisne, *Carter* 14084 (ISM). WHITE: SW. of Carmi, *Evers* 19888 (ILLS). WHITESIDE: Sinnissippi Park, Sterling, *V. Chase* 12937 (ILL). WILL: Braidwood, *Graham* 9932 (ISM). WILLIAMSON: Crab Orchard Lake, *Hardy* 50 (SIU). WINNEBAGO: Rockford, *E. Fell* 52-807 (ISM). WOODFORD: Four miles S. of Spring Bay, *V. Chase* 6216 (ISM).

10. CYPERUS ARISTATUS Rottb. Descr. & Icon. 6:23. 1773. (Fig. 11).
Cyperus inflexus Muehlenb. Descr. Gram. 16. 1817.
Cyperus aristatus var. *inflexus* (Muehlenb.) Boeckl. Linnaea 35:500. 1868.

Cespitose annual with an odor of *Ulmus rubra;* roots fibrous, forming a dense mat; culms 3-15 cm tall, very slender, purplish-tinged at base, smooth; leaves 2-3 on each culm, 0.5-1.5 mm wide; involucral bracts 2-4, all exceeding the inflorescence, the longest to 8 cm, 0.5-2.0 mm broad; spikes crowded into a sessile head-like cluster, occasionally with a few on rays up to 2.5 cm long; spikelets flattened, 6- to 18-

flowered, 3-9 mm long, 1-2 mm wide; scales oblong to oblong-lanceolate, prominently 7- to 9-nerved, 1-2 mm long with an outwardly curving acuminate tip 0.5-1.0 mm long, green when young becoming reddish-brown or brown at maturity; rhachilla wingless; stamen 1; style 3-cleft, deciduous; achenes trigonous, obovoid, minutely pebbled, 0.5-1.0 mm long, 0.3-0.5 mm broad, pale brown.

Habitat.—Moist soil along rivers, around lakes, or in fields.

Range.—Throughout most of North America, Mexico, South America.

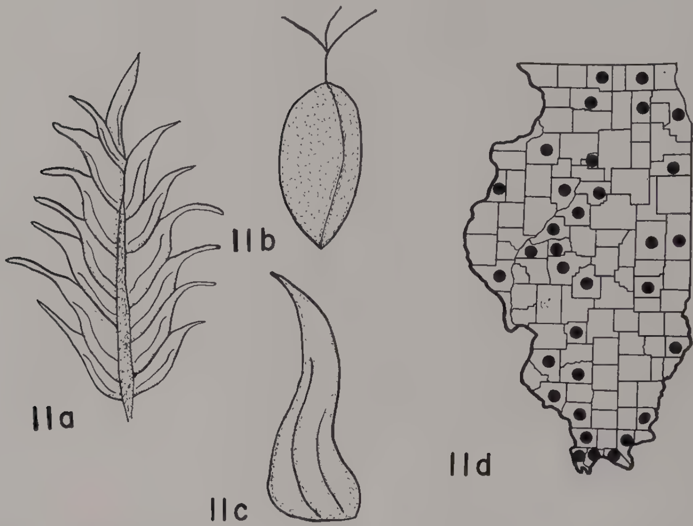
Kükenthal (1936), on the basis of somewhat shorter spikes and somewhat larger achenes, considers this species as a variety of the Old World *Cyperus aristatus* while Gleason (1952) makes no distinction between the two. O'Neill (1942) has amassed considerable data to show that the New World specimens are not distinct from Rottboell's entity.

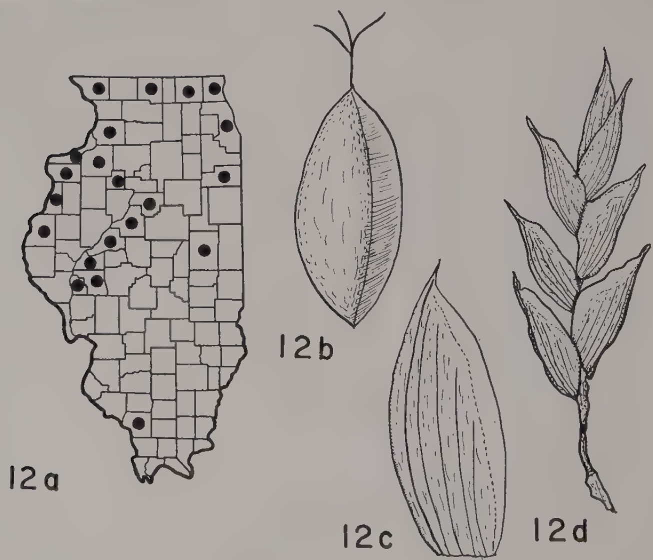
This species is scattered throughout Illinois in moist situations, particularly along the larger rivers. It occurs in moist depressions atop exposed sandstone bluffs in the southern counties.

Specimens Examined: ALEXANDER: W. of Sandusky, *Ahles* 4713 (ILL). BOND: Near Belvidere, *E. Fell* 54-1139 (ISM). CASS: Beardstown, *Rexroat* 3480 (ISM). CHAMPAIGN: Urbana, *Ahles* 6298 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). COLES: E. of Charleston, *Stover s.n.* (EI). COOK: Stoney Island, *A. Chase* 1996 (ILL). GALLATIN: One mile S. of Ridgway, *G. Dillard s.n.* (SIU). HENDERSON: Oquawka, *Patterson s.n.* (F). HENRY: N. of Penny Slough, *Dobbs* 9727 (ILLS). JACKSON: Between Crain & Grimsby, *Ahles* 5647 (ILL). KANE: Elgin, *Umbach s.n.* (ILL). KANKAKEE: Momence, collector unknown (ILL). LAWRENCE: NE. of Lawrenoeville, *Ahles* 4620 (ILL) MCHENRY: Algonquin, *Nason s.n.* (ILL). MACOUPIN: Carlinville, *Robertson* 9755 (ILLS). MASON: Six miles S. of Havana, *Rexroat* 3080 (ISM). MASSAC: Joppa, *Ahles* 6685 (ILL). MENARD: Athens, *Hall s.n.* (MO). OGLE: Oregon, *Moffatt s.n.* (ILL). PEORIA: Peoria, *McDonald s.n.* (ILL). PIKE: N. of Florence, *Evers* 21269 (ILLS). POPE: N. of Herod, *Ahles* 4684 (ILL). PULASKI: E. of Grand Chain, *Evers* 52503 (ILLS). PUTNAM: Lake Senachwine, *V. Chase* 10815 (ILL). RANDOLPH: Rock Castle Creek, *Bailey & Swayne* 1596 (SIU). ST. CLAIR: River shore, *H. Eggert s.n.* (MO). SANGAMON: Sangamon River, *Andrews s.n.* (ILL). TAZEWELL: Pekin, *V. Chase* 10851 (ILL). UNION: Union County State Forest, *Fuller* 797 (ILL). VERMILION: Kickapoo State Park, *Ahles* 3364 (ILL). WASHINGTON: Nashville, *French s.n.* (SIU). WINNEBAGO: Rockford, *E. Fell & G. Fell* 48-327 (ILL). WOODFORD: S. of Spring Bay, *V. Chase* 6213 (ILL).

11. CYPERUS SCHWEINITZII Torr. in Ann. Lyc. N. Y. 3.376. 1836. (Fig. 12).

Perennial with short rhizomes bearing corm-like swellings; culms 2-8 dm tall, usually scabrous, at least near the tip; leaves to 6 mm wide, seldom reaching the inflorescence, very scabrous along the margins, usually flat but occasionally revolute-margined; inflorescence with 1-2 oblong sessile spikes and 2-8 unequal rays over 8 cm long, with 3-6 scabrous-margined involucral bracts equalling or much exceeding the inflorescence; spikes ellipsoid to ovoid, with 5-15 very





Figs. 11 and 12. 11.—*Cyperus aristatus*. a. Spikelet, x 4. b. Achene, x 25. c. Scale, x 25. d. Map. 12.—*Cyperus schweinitzii*. a. Map. b. Achene, x 15. c. Scale, x 10. d. Spikelet, x 3.

ascending spikelets; spikelets flattened, 8- to 18-flowered, 12-25 mm long; scales ovate to rotund, with a mucro 0.5-1.5 mm long, with a scarious margin, 9- to 15-nerved, 2.5-4.0 mm long; rhachilla not winged; achenes trigonous, ellipsoid, 2.5-3.3 mm long, 1.0-1.2 mm broad, light brown.

Habitat.—Sandy soil.

Range.—Quebec to Idaho south to New Mexico, Illinois, northern Indiana, northern Ohio, and New Jersey.

Cyperus schweinitzii is most easily recognized by the mucro of the scales which is 0.5-1.5 mm long, the large achene (2.5-3.3 mm long), and the ascending spikelets. It is confused frequently with *C. filiculmis* var. *filiculmis*.

Specimens Examined: CASS: S. of Chandlerville, *Ahles* 2955 (ILL). CHAMPAIGN: E. of Urbana, *Buser* 1448 (ILL). COOK: Chicago, *Babcock* 3058 (ILL). HANCOCK: E. of Warsaw, *Evers* 38283 (ILLS). HENDERSON: Oquawka, *V. Chase* 5091 (ILL). HENRY: Four miles S. of Hooppole, *Dobbs* 9767 (ILLS). JACKSON: Along Gulf, Mobile, and Ohio Railroad, Murphysboro, *Mohlenbrock* 4514 (ILL). JO DAVIESS: Sandy banks of the Mississippi River, *Gleason & Gates* 2656 (ILL). KANKAKEE: SE. of Custer Park, *Steyermark* 64878 (F). LAKE: E. of Zion, *Brown* 165 (ILL). MCHENRY: Ringwood, *Vasey s.n.* (F). MASON: Havana, *Gleason s.n.* (ILL). MERCER: SE. of Keithsburg, *Evers* 48005 (ILLS). MORGAN: S. of Meredosia, *Evers* 41082 (ILLS). ROCK ISLAND: N. of Cordova, *Evers* 35466 (ILLS). SCOTT: N. of Bluffs, *Evers* 41066 (ILLS). STARK: N. of Duncan, *V. Chase* 793 (ILL). TAZEWELL: Near East Peoria, *V. Chase* 10770 (ILL). WHITESIDE: NW. of Erie, *Evers* 47618 (ILLS). WINNEBAGO: Rockford, *E. Fell & G. Fell* 48-341 (ILL). WOODFORD: Spring Bay, *V. Chase* 10002 (ILL).

12. CYPERUS HOUGHTONII Torr. Ann. Lyc. N. Y. 3:277. 1836. (Fig. 13).

Perennial with short rhizomes bearing corm-like swellings; culms 2-8 dm tall, smooth or nearly so; leaves to 4 mm wide, seldom reaching the inflorescence, usually with very smooth margins; inflorescence with 1 or 2 sessile spikes and 2-5 rays, with 2-5 usually smooth involucral bracts; spikes hemispherical, with ascending spikelets; spikelets flattened, 4- to 14-flowered, 5-22 mm long; scales rotund, obtuse and with a mucro, 11- to 15-nerved, 2.0-2.5 mm long, 1.0-1.5 mm broad; achenes trigonous, rounded below, nearly truncate above, 1.2-1.8 mm long, 0.8-1.2 mm broad, dark brown.

Habitat.—Sandy soil.

Range.—Quebec to Minnesota south to Iowa, northern Illinois, northern Indiana, and Virginia.

This species resembles *C. schweinitzii* but differs in its smaller achenes and its scales with only minute mucros. It differs from *C. filiculmis* var. *filiculmis* by its much broader achenes and scales.

C. houghtonii has been reported from Illinois by numerous authors, but almost all collections labelled as such in herbaria are actually either *C. schweinitzii* or *C. filiculmis* var. *filiculmis*.

Hunt s.n., which is probably adventive in Cook County, is the only

specimen seen during this study which can be referred to *C. houghtonii.* The natural range of this species probably should include Illinois, however.

Specimens Examined: COOK: South side of Chicago, *Hunt s.n.* (ILLS).

13. CYPERUS FILICULMIS Vahl, Enum. Pl. 2:328. 1806. (Fig. 14).

Perennial from hard corm-like rhizomes; culms very slender and wiry to somewhat more robust, to 8 dm tall, glabrous or slightly scabrous beneath the inflorescence; leaves flat or conduplicate, 1.0-5.5 mm wide, glabrous or with scabrous margins; inflorescence of a single sessile glomerule and sometimes with 1-several rays to 10 cm long, with up to 6 involucral bracts, some or all of which surpass the inflorescence; spikes hemispherical, but never completely spherical, with numerous radiating spikelets; spikelets 3- to 15-flowered, 3-20 mm long, with somewhat loose scales; scales acute or subacute, subcoriaceous, with hyaline margins, 5- to 9-nerved, 1.6-3.5 mm long; rhachilla wingless; style 3-cleft; achene trigonous, 1.3-2.0 (-2.2) mm long, 0.6-1.0 mm broad, black.

Two varieties occur in Illinois:

a. Plants with a central sessile glomerule and with 3-6 (-8) well-developed rays; spikelets (4-) 5- to 15-flowered; scales 2.4-3.5 mm long, some of the tips with a mucro 0.1-0.4 mm long; leaves 1.8-5.5 mm wide; achenes (1.7-) 1.8-2.2 mm long ....13a. *C. filiculmis* var. *filiculmis*

a. Plants with only a central sessile glomerule or occasionally with 1-2 rays; spikelets 3- to 8-flowered; scales 1.6-2.8 (-3.1) mm long, the tips acute or with a mucro less than 0.1 mm long; leaves 1.0-2.5 (-3.6) mm wide; achenes 1.2-1.8 (-2.0) mm long ....13b. *C. filiculmis* var. *macilentus*

13a. *Cyperus filiculmis* var. *filiculmis.*

Cyperus bushii Britton Man. Fl. North. U.S. 1044. 1901.

Cyperus mesochoreus Geise Am. Midl. Nat. 15:241-291. 1934.

Cyperus houghtonii Torr. var. *bushii* (Britton) Kükenth. *in* Kükenth., Pflanzenr. 20:469. 1936.

Cyperus houghtonii Torr. var. *uberior* Kükenth. *in* Kükenth., Pflanzenr. 20:469. 1936.

Much variation occurs among specimens of *Cyperus filiculmis.* The two varieties recognized in this study tend to intergrade with each other, but a general over-all largeness of *C. filiculmis* var. *filiculmis* separates the two.

Various specimens considered to be hybrids between *C. filiculmis* and *C. schweinitzii,* called *C. mesochoreus,* or perhaps between *C. filiculmis* and *C. houghtonii,* called *C. houghtonii* var. *uberior,* seem best treated as *C. filiculmis* var. *filiculmis.* These specimens have 7-15 flowers per spikelet, achenes 1.9-2.2 mm long, and usually some scabrosity on the culms beneath the inflorescence.

Confusion has arisen between *C. filiculmis* var. *filiculmis* and *C. schweinitzii.* The following table compares and contrasts some of the diagnostic characters:

	C. filiculmis var. *filiculmis*	*C. schweinitzii*
Mucro of scale	absent to 0.4 mm long	0.5-1.5 mm long
Culm	glabrous to moderately scabrous	harshly scabrous
Achene length	1.7-2.2 mm	2.5-3.3 mm
Spikelets	some ascending, some spreading, forming a hemispherical spike	all strongly ascending

Habitat.—Rocky or sandy soil.

Range.—Massachusetts to Michigan south to Nebraska, Texas, and Florida.

Specimens Examined: BOND: E. of Reno, *Evers* 18751 (ILLS). CASS: E. of Beardstown, *V. Chase* 11327 (ILL). CHAMPAIGN: Champaign, *Ahles* 6516 (ILL). COOK: Hyde Park, Chicago, *A. Chase* 1162 (ILL). HANCOCK: E. of Warsaw, *Evers* 38282 (ILLS). HENDERSON: W. of Lomax, *Evers* 18353 (ILLS). HENRY: *Dobbs* 17874a (ILLS). IROQUOIS: Five miles N. of Watseka, *Winterringer* 7050 (ISM). JO DAVIESS: SE. of East Dubuque, *Evers* 47490 (ILLS). KANKAKEE: Near St. Anne, *Jones* 16621 (ILL). LAKE: Three miles N. of Waukegan, *Fuller* 9031 (ISM). LEE: SE. of Amboy, *Evers* 49230 (ILLS). MCDONOUGH: *Myers* 111 (WI). MADISON: Wood River, *Evers* 38886 (ILLS). MARSHALL: Two miles N. of Lacon, *Evers* 39522 (ILLS). MASON: W. of Easton, *Evers* 47031 (ILLS). MENARD: SE. of Petersburg, *Evers* 45284 (ILLS). MERCER: SE. of Keithsburg, *Evers* 48011 (ILLS). OGLE: E. of Oregon, *Evers* 19370 (ILLS). ROCK ISLAND: Three miles NW. of Port Byron, *E. & G. Fell* F47-219 (ISM). SCHUYLER: S. of Browning, *Rexroat* 3090 (ISM). SCOTT: N. of Bluffs, *Evers* 41065 (ILLS). TAZEWELL: Pekin, *V. Chase* 10838 (ILL). WHITESIDE: N. of Fulton, *Ahles* 4243 (ILL). WILL: SE. of Wilmington, *Evers* 25568 (ILLS). WINNEBAGO: S. of Harrison Avenue, Rockford, *E. Fell* F48-348 (ISM). WOODFORD: S. of Spring Bay, *V. Chase* 10000 (ILL).

13b. *Cyperus filiculmis* var. *macilentus* Fern. Rhodora 8:128. 1906.

Cyperus macilentus Bickn. Bull. Torr. Club 35:478. 1908.

This slender phase of *C. filiculmis* more properly fits the epithet *filiculmis* than does the typical variety. In its most extreme form, the inflorescence of var. *macilentus* is reduced to a single sessile spike, the leaves are 1.1-1.4 mm wide, the scales 2.0-2.6 mm long, the achene 1.3-1.6 mm long, and the spikelets 3- to 6-flowered.

Some difficulty in distinguishing the two varieties is due in part to the fact that immature specimens of var. *filiculmis* strongly resemble mature var. *macilentus*. There is no doubt, however, that the two varieties intergrade considerably.

Habitat.—Sandy soil.

Range.—Similar to var. *filiculmis*, perhaps reaching somewhat farther south.

Specimens Examined: ADAMS: Quincy, *Evers* 906 (ILL). BOONE: W. of Belvidere, *E. Fell* 52655 (ISM). BUREAU: *Pepoon & Barrett* 6104 (ILLS). CALHOUN: NW. of Belleview, *Evers* 27247 (ILLS). CASS: Beardstown, *V. Chase*

11343 (ILL). CHAMPAIGN: Champaign, *Ahles* 6292 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). COOK: Chicago, *A. Chase* 1188 (ILL). FULTON: Canton, *collector unknown* (ILL). GALLATIN: S. of Kedron, *Evers* 26777 (ILLS). HARDIN: E. of Lamb, *Evers* 45055 (ILLS). HENDERSON: N. of Oquawka, *Evers* 39754 (ILLS). HENRY: Dobbs 12875 (ILLS). IROQUOIS: N. of Donovan, *Ahles* 6878 (ILL). JACKSON: Ten miles NW. of Murphysboro, *Bailey & Swayne* 1512 (SIU). JERSEY: Pere Marquette State Park, *Fuller s.n.* (ISM). JO DAVIESS: S. of Hanover, *Steyermark* 40804a (ILL). JOHNSON: Near Buncombe, *Buser s.n.* (ILLS). KANE: Elgin, *Sherff* 1942 (ILL). KANKAKEE: Rock Creek, *Jones* 15879 (ILL). LAKE: Illinois Beach State Park, *Brown* 210 (ILL). LASALLE: Starved Rock State Park, *V. Chase* 10157 (ILL). LAWRENCE: E. of Billet, *Evers* 34720 (ILLS). LEE: Six miles NW. of Franklin Grove, *Keithley* 252 (ISM). MCDONOUGH: Pleasant Valley, *Myers* 568 (SIU). MCHENRY: Ringwood, *Vasey s.n.* (ILL). MADISON: Wood River, *Evers* 38885 (ILLS). MARSHALL: Two miles N. of Lacon, *Evers* 39509 (ILLS). MASON: E. of Havana, *V. Chase* 4016 (ILL). MENARD: S.E. of Petersburg, *Evers* 45274 (ILLS). MONROE: S. of Fults, *Bailey & Swayne s.n.* (ISM). MORGAN: N. of Meredosia, *Rexroat* 2070 (ISM). OGLE: Near Castle Rock, *Fuller* 10916 (ISM). PEORIA: Peoria, *V. Chase* 4530 (ILL). PIKE: Three miles S. of Kinderhook, *Evers* 24725 (ILLS). PUTNAM: S.E. of Putnam, *V. Chase* 16870 (ILL). RANDOLPH: E. of Marissa, *Bailey & Swayne s.n.* (SIU). ROCK ISLAND: NW. of Port Byron, *E. & G. Fell s.n.* (ISM). ST. CLAIR: Near Dupo, *Neill* 926 (ISM). SANGAMON: Clear Lake, *Fuller* 5657 (ISM). SCHUYLER: *Rexroat* 1711 (ISM). SCOTT: N. of Bluffs, *Evers* 24992 (ILLS). TAZEWELL: Pekin, *V. Chase* 12875 (ILL). WABASH: Palmyra, *Schneck s.n.* (ILL). WASHINGTON: One mile W. of Addieville, *Boewe* 17283 (ILLS). WHITE: NE. of Carmi, *Evers* 11242 (ILLS). WHITESIDE: N. of Fulton, *Ahles* 4241 (ILL). WILL: SE. of Wilmington, *Evers* 25560 (ILLS). WINNEBAGO: S. of Rockford, *Fuller* 2347-H (ISM). WOODFORD: Spring Bay, *V. Chase s.n.* (ILL).

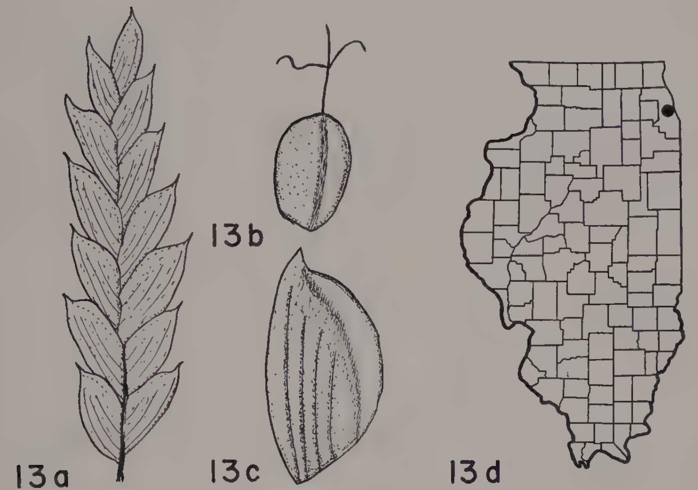
14. CYPERUS GRAYIOIDES Mohl. Brittonia 11:255-256. 1959. (Fig. 15).

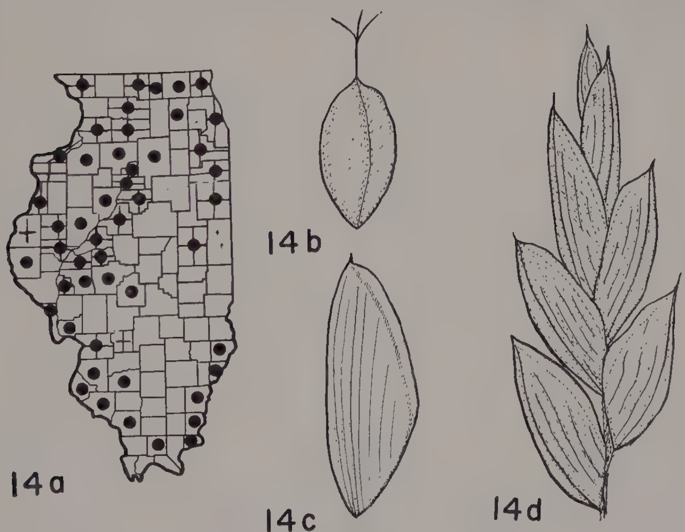
Perennial from a short horizontal rhizome; culms 30-60 cm tall, 0.7-1.2 mm broad, glabrous; leaves conduplicate, 2.0-3.5 mm wide, shorter than the culm, glabrous; inflorescence with 3-8 rays and 4-7 conduplicate bracts; spikes spherical, with numerous spikelets radiating in all directions; spikelets 4- to 7-flowered, to 10 mm long; scales loosely imbricate, somewhat remote, obtuse, the terminal scale acute, 9- to 13-nerved, 2.2-2.8 mm long; rhachilla wingless; stamens 3; styles 3-cleft; achene trigonous, oblongoid to broadly oblongloid, long apiculate, 2.0-2.6 mm long, black.

Habitat.—Sand prairies and blowouts.

Range.—Central and northwestern Illinois.

This species derives its name from the striking resemblance of it to the east coast *Cyperus grayii*. The two are similar in that the inflorescence is comprised of a sessile terminal head and usually five to several long peduncled heads which have the spikelets radiating in all directions. The unwinged rhachilla, the hyaline-margined scales, and the larger achenes separates this Illinois endemic from *C. grayii*. *Cyperus grayioides* resembles *C. filiculmis* on the basis of the hyaline





Figs 13 and 14. 13.—*Cyperus houghtonii.* a. Spikelet, x 3. b. Achene, x 10. c. Scale, x 15. d. Map. 14.—*Cyperus filiculmis.* a. Map: circle indicates var. *macilentus,* cross indicates var. *filiculmis.* b. Achene, x 10. c. Scale, x 15. d. Spikelet, x 4.

scales, but differs in that *C. grayioides* has larger achenes, spikelets radiating in all directions, and more loosely disposed scales. The resemblance to *C. schweinitzii* is even less.

This endemic species grows in pure sand along the Illinois River and in a sand prairie in northwestern Illinois.

Specimens Examined: MASON: Blow sand, August 22, 1954, *Rexroat* 1125 (holotype — ISM); Havana, bunch-grass association, August 13, 1903, *Gleason* 1047 (ILL). WHITESIDE: Sand prairie N. of Fulton, August 15, 1952, *Evers* 35442 (ILLS); blowout in sand prairie, N. of Fulton, August 15, 1952, *Evers* 35459 (ILLS).

15. CYPERUS LANCASTRIENSIS Porter ex A. Gray, Man. Bot., ed. 5:555. 1867. (Fig. 16).

Perennial with short rhizomes bearing one or more corm-like swellings; culms 3-60 cm tall, smooth; leaves to 10 mm broad, somewhat shorter than the culm, glabrous; inflorescence with 5-12 well-developed rays, with 6-10 involucral bracts, some of which surpass the rays; spikes short cylindric, with numerous horizontally radiating or reflexed spikelets; spikelets subulate, 3- to 6-flowered, 7-10 mm long; scales narrowly oblong, obtuse to subacute, closely appressed, 3.5-4.5 mm long, 7- to 13-nerved, yellowish; achenes trigonous, narrowly oblongoid, 2.0-2.6 mm long, 0.5-0.8 mm broad.

Habitat.—Moist and often sandy woods.

Range.—New Jersey to Ohio and Wisconsin south to Arkansas and Georgia.

In several ways, *C. lancastriensis* resembles *C. strigosus* but it can easily be distinguished by its longer achenes and usually reflexed spikelets.

The range of *C. lancastriensis* in Illinois is limited to the extreme southern tip where it is very rare. It was not known from Illinois until 1949. Specimens recorded in the literature from Jackson County are actually *C. strigosus*.

Specimens Examined: MASSAC: E. of Joppa, *Evers* 19952 (ILLS). PULASKI: One-half mile N. of Douglas Landing, *Evers* 5159 (ILLS).

16. CYPERUS OVULARIS (Michx.) Torr. Ann. Lyc. N. Y. 3:278. 1836. (Fig. 17).

Kyllinga ovularis Michx. Fl. Bor. Am. 1:29. 1803.

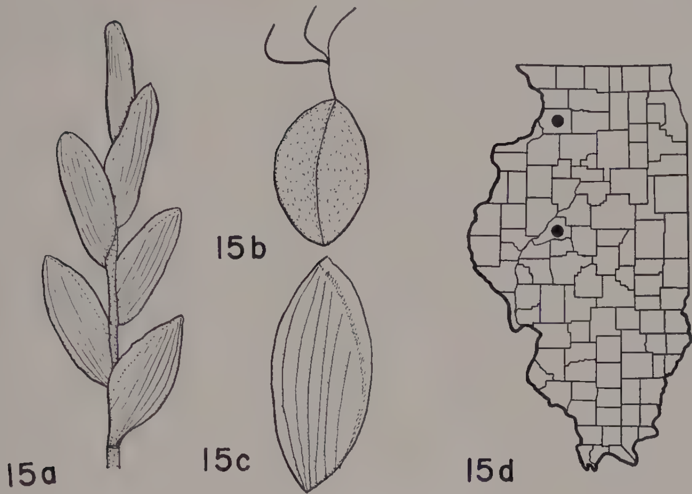
Cyperus ovularis var. *robustus* Britt. Bull. Torr. Club 13:214. 1886, *non* Boeckl. Linnaea 36:378. 1870.

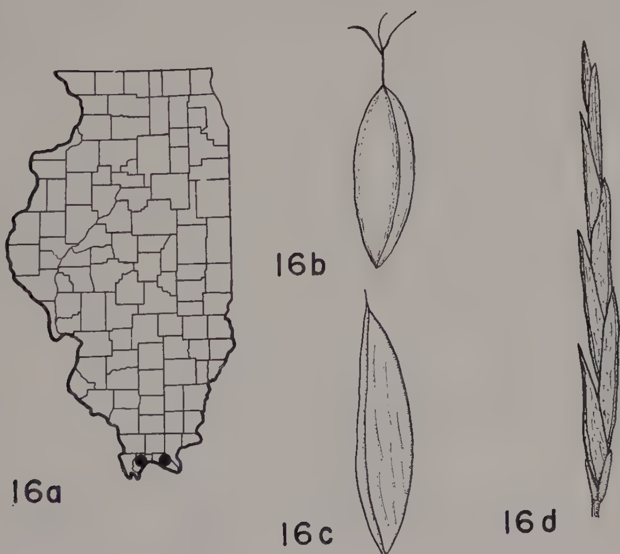
Cyperus ovularis var. *sphaericus* Boeckl. Linnaea 36:378. 1870.

Cyperus wolfii Wood Bull. Torr. Club. 6:72. 1876.

Cyperus ovularis var. *wolfii* (Wood) Kükenth. Pflanzenr. 20:512. 1936.

Perennial from short rhizomes bearing corm-like swellings; culms smooth, 2.5-10.0 cm tall; leaves flat or rarely revolute, to 10 mm broad, much shorter than the culm, scabrous; inflorescence with a single sessile spike and usually 2-12 unequally ascending rays to 10 cm long, with 4-7 involucral bracts, the longest much exceeding the in-





Figs. 15 and 16. 15.—*Cyperus grayioides*. a. Spikelet, x 5. b. Achene, x 10. c. Scale, x 15. d. Map. 16.—*Cyperus lancastriensis*. a. Map. b. Achene, x 10. c. Scale, x 8. d. Spikelet, x 5.

florescence; spikes dense, globose, 8-20 mm in diameter; spikelets very numerous, radiating in all directions, 2- to 3-flowered, linear-lanceolate, 3-8 mm long; scales oblong, obtuse, 7- to 13-nerved, closely appressed, 3-4 mm long; achenes trigonous, oblongoid, apiculate, brown, 1.8-2.2 mm long, less than 1 mm broad.

Habitat.—Dry sandy woods, old fields.

Range.—New York to South Dakota south to Texas and Florida.

Cyperus ovularis is a most variable species. Numerous intergradient varieties and forms have been proposed, but lines of demarcation separating them are nonexistent. Var. *sphaericus* Boeckl. refers to specimens which, on the average, are smaller than the typical variety. At the other extreme exceedingly robust specimens have sometimes been segregated as var. *robustus* Britt. (*non* Boeckl.) or var. *wolfii* (Wood) Kükenth. Since all intergradations may be found from the smallest to the most robust specimens, it does not seem advisable to retain the varieties. Some Illinois material, notably *Mohlenbrock & Voigt* (Pope County) and *Mohlenbrock 10009* (Jackson County), requires a change in the range of certain characters over that given in current manuals. These specimens have up to 12 rays with spikes that measure 20 mm in diameter. One specimen from Jackson County, bearing merely a single sessile glomerule, resembles *C. filiculmis* var. *macilentus*, but differs in its very obtuse scales.

Specimens Examined: ALEXANDER: E. of Thebes, *Franklin* 13 (ILL). BOND: One mile N. of Waburn, *Evers* 39305 (ILLS). CLAY: S. of Flora, *Winterringer* 6052 (ISM). EDWARDS: N. of Albion, *Evers* 20197 (ILLS). FRANKLIN: N. of Benton, *Ahles* 5536 (ILL). GALLATIN: N. of Ridgway, *Evers* 34398 (ILLS). HARDIN: Six miles N. of Eichorn, *Ahles* 2753 (ILL). JACKSON: NW. of Makanda, *Cranwill s.n.* (ILL). JEFFERSON: S. of Mount Vernon, *Evers* 5494 (ILL). JOHNSON: Ozark, *Winterringer* 4061 (ISM). LAWRENCE: Lawrenceville, *Sivert s.n.* (ILL). MARION: Kell, *Burrill s.n.* (ILL). MASSAC: Metropolis, *Ahles* 2803 (ILL). MONROE: SE. of Poe, *Evers* 20506 (ILLS). PEORIA: Peoria, *Brendel s.n.* (ILL). PERRY: E. of Rice, *Evers* 12415 (ILLS). POPE: N. of Herod, *Winterringer* 5975 (ISM). RANDOLPH: Chester, *Winterringer* 3841 (ISM). RICHLAND: Olney, *Sherer* 621 (ILL). ST. CLAIR: Near French Village, *Fuller* 13143 (ISM). SALINE: SE. of Rudement, *Winterringer* 3515 (ISM). UNION: Between Ware and Wolf Lake, *Winterringer* 3458 (ISM). WABASH: Mt. Carmel, *Schneck s.n.* (ILL). WASHINGTON: N. of New Minden, *Winterringer* 3845 (ISM). WAYNE: E. of Geff, *Walker* 23 (ILL). WHITE: Norris City, *Ahles* 4677 (ILL). WILLIAMSON: Near Herrin, *Pepoon & Barrett s.n.* (ILLS).

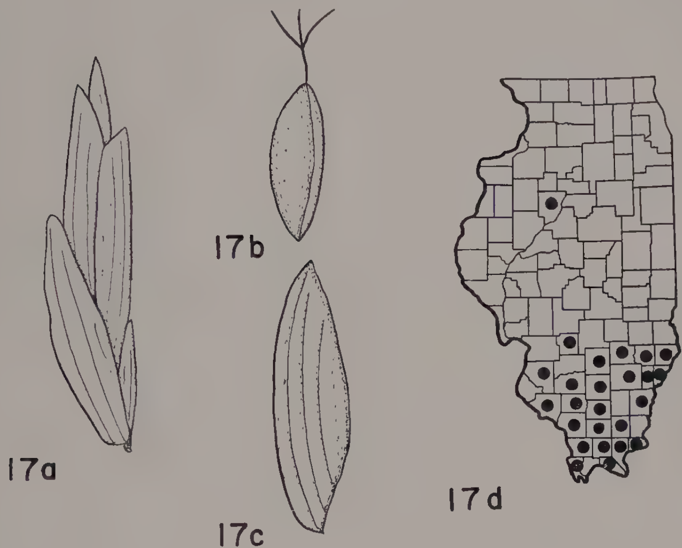
17. CYPERUS DENSICAESPITOSUS Mattf. & Kükenth. *in* Kükenth., Pflanzenr. 20:597. 1936. (Fig. 18).

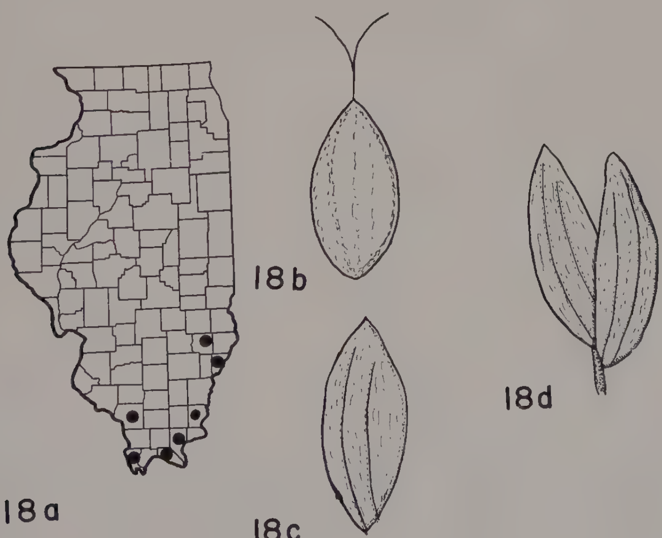
Kyllinga pumila Michx. Fl. Bor. Am. 1:28. 1803.

Kyllinga tenuifolia Steud. Syn. Pl. Cyp. 69. 1899.

Cyperus tenuifolius (Steud.) Dandy *in* Exell, Cat. Vasc. Pl. S. Tome 363. 1944, *non C. tenuifolius* Walp.

Sweet-smelling annual, cespitose, with fibrous roots; culms slender, 5-30 cm tall, smooth; leaves flat, soft, 1-3 mm wide, smooth, with the





Figs. 17 and 18. 17.—*Cyperus ovularis.* a. Spikelet, x 8. b. Achene, x 10. c. Scale, x 10. d. Map. 18.—*Cyperus densicaespitosus.* a. Map. b. Achene, x 25. c. Scale, x 20. d. Spikelet, x 20.

lower sheaths bladeless; inflorescence of 1 (-3) subglobose, sessile spikes 4-10 mm long and nearly as broad, with 2-4 spreading bracts to 10 cm long; spikes with numerous spikelets; spikelets 2-ranked, 1-flowered, 1.5-2.5 mm long; scales ovate, acute, with a distinct keel and hyaline margin, 1.5-2.2 mm long, the upper sterile; stamens 2; styles 2; achene lenticular, ellipsoid, 0.8-1.0 mm long, 0.5 mm wide.

Habitat.—Moist, open soil.

Range.—New York to Kansas south to Texas and Florida; Mexico; South America; Africa.

The presence of a single fertile flower per spikelet has been used by previous workers to separate the genus *Kyllinga* from *Cyperus*. There is little other reason to recommend this segregation. Fernald (1950), following Dandy (1944), calls this species *Cyperus tenuifolius*, but this is not the same entity which Walpole meant when he first used this combination many years earlier. Thus the epithet proposed by Mattfeld and Kükenthal is the first legitimate one applied to this species.

The fragrant odor given off by this plant frequently indicates its presence to the collector before it is actually observed.

Specimens Examined: ALEXANDER: Two and one-half miles NW. of Tamms, *Buser* 5374 (ILLS). GALLATIN: One-half mile S. of Ridgway, *G. Dillard s.n.* (SIU). JACKSON: Giant City State Park, *Mohlenbrock* 552 (SIU). MASSAC: E. of Joppa, *Evers* 19947 (ILLS). POPE: Bay bottoms, *Bailey & Swayne* 2875 (ILLS). WABASH: Mt. Carmel, *Patterson s.n.* (F).

18. CYPERUS FERRUGINESCENS Boeckl. in Linnaea 36:396. 1870. (Fig. 19).

Cyperus ferax sensu Pepoon 194. 1927, *non* L. C. Rich. Act. Soc. Hist. Nat. Paris 1:106. 1792, in part.

Cyperus michauxianus sensu Lapham 542. 1857, *non* Schult. *in* Roem. & Schult., Mant. 2:123. 1824.

Cyperus speciosus Vahl, Enum. 2:364. 1806.

Cyperus speciosus Vahl var. *squarrosus* Britt. Bull. Torr. Club 13:214. 1886.

Cyperus ferax L. C. Rich. subsp. *speciosus* (Vahl) Kükenth. var. *squarrosus* (Britt.) Kükenth. Pflanzenr. 20:620. 1936.

Cyperus odoratus sensu Gleason 251. 1952, *non* L. Sp. Pl. 46. 1753.

Coarse annual with fibrous roots; culms to 1 m tall, smooth; leaves flat, usually not equalling the culm, to 12 mm broad; inflorescence with 1-2 sessile heads and 2-12 simple or compound rays, with several of the numerous involucral bracts surpassing the inflorescence; spikes cylindric, with numerous horizontally radiating or ascending spikelets; spikelets flattened, 8- to 25-flowered, to 25 mm long with appressed or rarely loosely spreading scales; scales ovate, 1.7-3.0 mm long, with numerous faint nerves, reddish-brown or golden-brown, the terminal scale often subulate; rhachilla winged; achene obovoid-oblong, 1.0-1.7 mm long, red-brown or brown.

Habitat.—Rich moist soil.

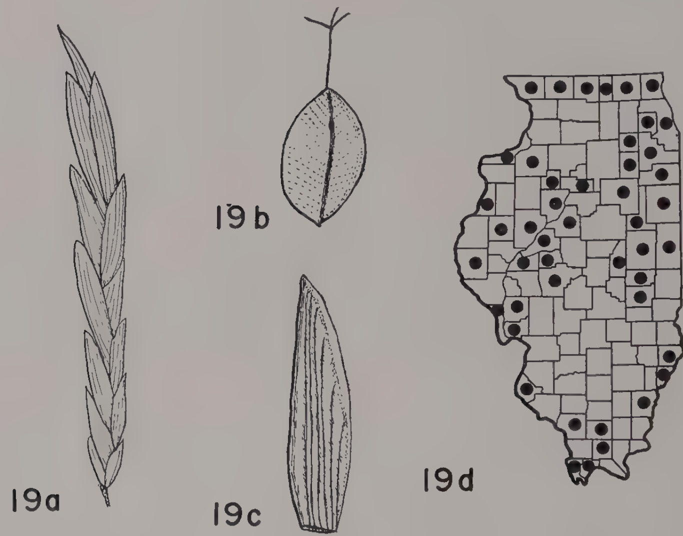
Range.—Massachusetts to Oregon south to California and Alabama.

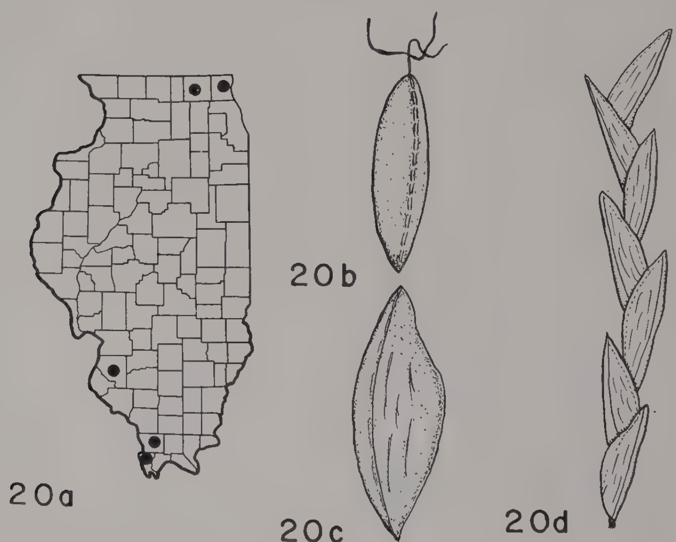
The correct nomenclature for this species has been in a state of confusion for years. If Linnaeus' *C. odoratus,* interpreted as being distinct because of its black achenes 1.5-2.0 mm long, is different from the Illinois material, than *Cyperus ferruginescens* Boeckl. is the first legitimate binomial.

Cyperus odoratus, in the restricted sense, is a species of southeastern United States and Tropical America.

Cyperus ferruginescens is a species subjected to frequent inundations which gives rise to peculiar individuals 1-20 cm tall with spikelets to 25 mm long and scales 2.5-3.0 mm long and very loosely spreading. The subulate terminal scales of this species help to distinguish it from *C. esculentus.*

Specimens Examined: ADAMS: Quincy, *Evers* 790 (ILL). BOONE: Belvidere, *E. Fell s.n.* (ISM). BROWN: E. of Cooperstown, *Evers* 40558 (ILLS). BUREAU: E. of Mineral, *Evers* 21211 (ILLS). CALHOUN: N. of Hardin, *Evers* 21417 (ILLS). CASS: S. of Beardstown, *Evers* 21390 (ILLS). CHAMPAIGN: Near Champaign, *Burrill & Sparrow* 14206½ (ILL). COLES: Lake Charleston, *Stover s.n.* (EI). COOK: South Chicago, *Sherff* 1766 (ILL). DOUGLAS: Villa Grove, *Evers* 52039 (ILLS). DUPAGE: Five miles S. of Downers Grove, *Evers* 32144 (ILLS). FORD: Paxton, *Moffatt* 509 (ILL). FULTON: Duck Island, *V. Chase* 4711 (ILL). GREENE: N. of Carrollton, *Winterringer* 12737 (ISM). GRUNDY: SW. of Gardner, *Evers* 21681 (ILLS). HANCOCK: S. of Nauvoo, *Evers* 20938 (ILLS). HENDERSON: N. of Oquawka, *Evers* 21013 (ILLS). HENRY: N. of Green River Station, *Dobbs* 9771 (ILLS). IROQUOIS: Gilman, *collector unknown* (ILL). JACKSON: Grand Tower, *Gleason s.n.* (ILL). JERSEY: Pere Marquette State Park, *Fuller* 542 (ISM). JO DAVIESS: S. of Blanding, *Evers* 36228 (ILLS). JOHNSON: E. of Vienna, *Evers* 32948 (ILLS). KANKAKEE: Wet grounds, *collector unknown* (ILL). KENDALL: NE. of Millington, *Evers* 40347 (ILLS). LAKE: Lake Villa, *Graham* 9419 (ISM). LAWRENCE: Lawrenceville, *Winterringer* 6963 (ISM). LIVINGSTON: One mile W. of Pontiac, *Fuller* 9170 (ISM). MCDONOUGH: N. of Bushnell, *Myers* 1170a (ISM). MCHENRY: Ringwood, *Vasey s.n.* (ILL). MCLEAN: Locality unknown, *Fuller* 299 (ISM). MARSHALL: S. of Sparland, *Evers* 19532 (ILLS). MASON: Cuba Island, *Anderson & Hawkins* 9773 (ILLS). MENARD: Athens, *Hall s.n.* (F). MONROE: S. of Fults, *Bailey & Swayne* 2806 (SIU). PEORIA: Peoria, *McDonald* 61 (ILL). PIATT: Monticello, *Seymour s.n.* (ILL). PULASKI: E. of Grand Chain, *Evers* 52506 (ILLS). ROCK ISLAND: Osburn, *Seymour s.n.* (ILL). SANGAMON: Curran, *Fuller* 6748 (ISM). SCHUYLER: SW. of Frederick, *Evers* 40507 (ILLS). SCOTT: W. of Winchester, *Evers* 20246 (ILLS). STARK: Near Wady Petra, *V. Chase* 784 (ILL). STEPHENSON: Near Freeport, *Serb* 9791 (ISM). TAZEWELL: Near East Peoria, *V. Chase* 3300 (ILL). VERMILION: Vermilion River, *G. Jones* 16244 (ILL). WABASH: Palmyra, *Schneck s.n.* (ILL). WHITE: Five miles E. of Crossville, *Winterringer* 6925 (ISM). WILL: Near Braidwood, *Graham* 9932 (ISM). WILLIAMSON: Carterville strip mine, *Bell s.n.* (SIU). WINNEBAGO: Rockford, *Fuller & Haime* 6F (ISM).





Figs. 19 and 20. 19.—*Cyperus ferruginescens.* a. Spikelet, x 3. b. Achene, x 15. c. Scale, x 15. d. Map. 20.—*Cyperus engelmannii.* a. Map. b. Achene, x 15. c. Scale, x 15. d. Spikelet, x 5.

19. CYPERUS ENGELMANNII Steud. Syn. Pl. Cyp. 47. 1855. (Fig. 20).
Cyperus ferax L. C. Rich. subsp. *engelmanni* (Steud.) Kükenth. Pflanzenr. 20:620. 1936.

Rather coarse annual with fibrous roots; culms to 60 cm tall, smooth; leaves to 6 mm wide, usually exceeding the culm, smooth; inflorescence of 1-several sessile spikes and 1-5 rays, with up to 6 involucral bracts much surpassing the inflorescence; spikes ellipsoid to oblongoid, with numerous horizontally radiating or ascending spikelets; spikelets terete, slender, to 18-flowered, 10-20 mm long, the flowers remote; scales brown, or reddish, ovate-lanceolate, acute, 2.2-3.0 mm long, with 7-13 rather faint nerves, the tip of one barely reaching the base of the one above it on the same side, thereby giving the spikelet a rather zigzag appearance; rhachilla winged; achenes linear-oblong, 1.5-2.2 mm long.

Habitat.—Wet ground.

Range.—Massachusetts and Minnesota south to Nebraska and Virginia.

Kükenthal (1936) maintains that this is nothing more than a sparsely-flowered variety of *Cyperus ferax*. The uniquely peculiar arrangement of the scales, however, seems to indicate the necessity for separating *C. engelmannii* as a distinct species.

Several Illinois collections previously referred to this are actually *C. ferruginescens*. Only a very few stations are known for *C. engelmannii* in Illinois, where it must be considered exceedingly rare. The type locality, usually attributed to St. Louis, Missouri, is actually based on an Engelmann collection along Cahokia Creek opposite St. Louis in St. Clair County, Illinois.

Specimens Examined: ALEXANDER: Horseshoe Lake S. of Olive Branch, *Evers* 41483 (ILLS). LAKE: Cedar Lake, *Gleason & Shobe* 153 (ILL). MCHENRY: Ringwood, *Vasey s.n.* (F). ST. CLAIR: Cahokia Creek, *Engelmann s.n.* (MO). UNION: S. of Ware, along Route 146, *Pepoon & Barrett s.n.* (ILLS).

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A Synopsis of the Cave Beetles of the Genus Pseudanophthalmus of the Mitchell Plain in Southern Indiana (Coleoptera, Carabidae)

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Thirteen species and subspecies of cave beetles of the genus *Pseudanophthalmus* Jeannel have been reported from the Mitchell Plain of southern Indiana. Horn (1871, 1883), Jeannel (1931, 1949), and Krekeler (1958) have described and illustrated the majority of these forms in considerable detail. The present paper is intended to be used in conjunction with the papers of Jeannel (1949) and Krekeler (1958), and no attempt has been made to repeat descriptions of forms which have been adequately treated by these authors. The discovery of a "lost" species in Wyandotte Cave and a nearby cavern necessitates a new combination and the changing of several trinomials. A new species, from Lawrence County, is described.

For reasons stated in an earlier paper (Barr, 1959) the writer has applied the polytypic species concept to the systematics of *Pseudanophthalmus* and other genera of troglobious carabids. An alternative taxonomic approach was offered by Krekeler (1958), who regarded each morphologically distinct cave population (or group of similar populations in closely associated caves) as genetically isolated.

The specimens upon which the present paper is based were collected in Crawford, Harrison, Lawrence, Monroe, Orange, Owen, and Washington Counties, Indiana, during the summer of 1957 and the fall of 1958. Dr. Carl H. Krekeler, Valparaiso University, whose recent (1958) paper is the most important single contribution to our knowledge of Indiana anophthalmids, provided a topotype *P. morrisoni* and a paratype *P. youngi donaldsoni* for examination. One *P. morrisoni* and six *P. youngi donaldsoni* were collected for the writer by Mr. Thomas L. Poulson.

Deep appreciation is expressed to Mr. Lewis D. Lamon, Corydon, Indiana, and to Miss Leona Hert, Springville, Indiana, for assistance in collecting the material discussed below. Mr. Robert Louden, manager of Wyandotte Cave, was most courteous and helpful. Dr. Harold J. Grant, Academy of Natural Sciences of Philadelphia, kindly compared the writer's topotypes with Horn's types of *Anophthalmus eremita* and *A. tenuis*.

Five species groups and six species are recognized in the present study, four of the groups being monotypic. The species may be separated by the following key.

KEY TO KNOWN SPECIES OF PSEUDANOPHTHALMUS OF THE MITCHELL PLAIN IN SOUTHERN INDIANA

1 Posterior pronotal angles small or quadrangular, not projecting posterior to the base of the pronotum; median lobe of labrum not prominent.......... 2

1′ Posterior pronotal angles acute, produced backward beyond the base of the pronotum; medium lobe of labrum well defined, prominent................ 4

2 Size medium (3.8-4.9 mm) or large (5.3-5.4 mm); longitudinal elytral striation absent or very indistinct.. 3

2′ Size small (3.2-3.8 mm); longitudinal elytral striation shallow but distinct (Lawrence County) .... *P. leonae* n. sp.

3 Size medium (3.8-4.9 mm); longitudinal striation of elytra present but indistinct (Lawrence County) .... *P. emersoni* Krekeler

3′ Size large (5.3-5.4 mm); longitudinal striation of elytra completely absent, disc strongly alutaceous (Crawford and Harrison Counties)................... .... *P. eremita* (Horn)

4 Right copulatory piece a broad, curved membrane, concave dorsally when seen in lateral view (Fig. 1); left piece a rolled, membranous rod; recurved portion of apical stria usually (but not always) running into the third longitudinal stria (Crawford, Harrison, Lawrence, Orange, Washington Counties)...*P. tenuis* (Horn) new comb.

4′ Transfer apparatus not as described above; recurved portion of apical stria usually (but not always) directed toward the fifth longitudinal stria 5

5 Transfer apparatus a tube, the left dorsal piece half the size of the right ventral piece; apex of right ventral piece projecting beyond the left dorsal, shaped like the bow of a canoe (Fig. 2) (Washington and Lawrence Counties) .... *P. youngi* Krekeler

5′ Transfer apparatus of two sinistrally concave, spatulate copulatory pieces (Fig. 3) which form a spout, the left dorsal piece smaller and nested within the right ventral piece (Lawrence, Monroe, and Owen Counties) .... *P. shilohensis* Krekeler

EREMITA GROUP

Pseudanophthalmus eremita (Horn)
Figs. 4, 7

Anophthalmus eremita Horn 1871: 325. Horn 1883: 272. Leng 1920: 55. Type: Wyandotte Cave, Crawford Co., Indiana (Acad. Nat. Sci. Philadelphia).

Not *Pseudanophthalmus eremita* of Jeannel 1928: 131. Jeannel 1931: 466. Valentine 1932: 275. Jeannel 1949: 56. Krekeler 1958: 170.

P. eremita (Horn) is known from only three specimens, all males: (1) the type, collected by E. D. Cope in Wyandotte Cave; (2) one specimen, Langdon's Cave, Harrison Co., Indiana (July 14, 1957, T.C.B.); and (3) one specimen, Wyandotte Cave (October 26, 1958, L. D. Lamon, L. D. Lamon, Jr., and T. C. B.). Female unknown.

Although Horn's descriptions (1871, 1883) of *eremita* and *tenuis* are explicit and adequate for differentiation of the two species, the rarity of the former apparently led to the supposition that only one

species inhabited Wyandotte Cave. *Anophthalmus tenuis* Horn was listed as a synonym of *A. eremita* by Leng (1920) and most later authors followed suit. The present author has avoided committing the same error purely through a happy circumstance — the discovery of both forms in Langdon's Cave, 2.4 miles SE. of Wyandotte, which induced him to conduct an extensive search for beetles in the type cave. A six-hour collecting trip yielded thirty specimens, twenty-nine of which were *tenuis* and one of which was *eremita*. A description of this specimen, a late teneral, follows.

Length 5.3 mm. Form robust and rather depressed. Color pale, yellow, testaceous. Head of moderate proportions (1.15 x 0.83 mm, index 0.72); labrum doubly emarginate, the median lobe low but well defined. Pronotum transverse (0.92 x 1.10 mm, index 1.20), subconvex, sparsely pubescent; greatest width at anterior setae, behind which the sides curve very gently back to the shallow basal sinus; posterior angles blunt, almost quadrangular. Elytra elongate-oval (2.85 x 1.84 mm, index 0.65), tapered apically, with a small cauda; surface wholly devoid of longitudinal striae, strongly alutaceous; rows of punctations faintly visible; pubescence sparse, locally arranged in longitudinal rows; humeri prominent, rounded, serrulate, setose; humeral set of setae closely spaced, resulting in a high chaetotaxial index (0.63); first discal seta posterior to fourth marginal puncture; apical recurrent stria broadly arcuate, turning abruptly and running to the third discal puncture. Aedeagus (Fig. 4) long and slender (1.19 mm); basal bulb very large and strongly flexed; basal keel absent; median lobe straight posterior to basal flexure; apex abruptly produced into a long, blunt spine on the left (dorsal, *in situ*) side, with a slight enlargement at the end; transfer apparatus of two elongate, rod-like copulatory pieces with blunt, rounded apices; left piece a little longer and narrower than right piece; internal sac armed with dense rows of small scales; parameres long, bearing four long, stout setae. Antennae of moderate length (3.54 mm, antennal index 0.66).

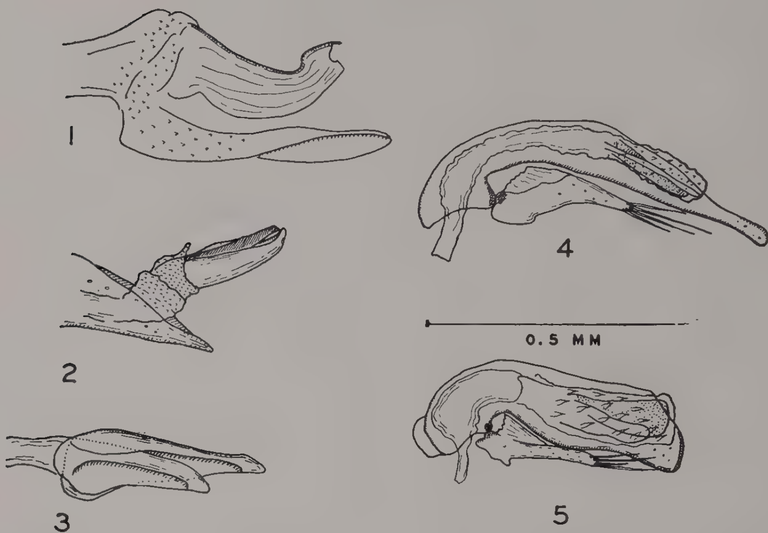
The specimen from Langdon's Cave (Fig. 7) differs in minor particulars: (1) it is fully sclerotized; (2) the elytra are not caudate; (3) the aedeagus bears a small basal keel and is slightly thicker in the middle portion, though of nearly the same length (1.17 mm). Like the topotype described above, the type male is caudate (H. J. Grant, pers. comm.). The writer has seen caudate elytra elsewhere in the genus only in a single *P. s. shilohensis* Krekeler.

Pseudanophthalmus emersoni Krekeler

Pseudanophthalmus emersoni Krekeler 1958: 176. Type: Donnehue's Cave, Lawrence Co., Indiana (Chicago Nat. Hist. Mus.).

P. emersoni is known only from the type locality (C. H. Krekeler and W. W. Bloom, 1950; C. H. Krekeler, 1953; T. C. B., 1957) where it coexists with *P. s. shilohensis*. It is apparently not very abundant.

With *eremita*, this species shares group characters — sparsely pubescent pronotum and elytra; trilobate labrum; transverse pronotum with quadrate hind angles; obsolescent elytral striation; and the nature of the apical recurrent stria and aedeagus. The position of the first discal stria is well behind the level of the fourth marginal puncture in both *eremita* and *emersoni*.



Figs. 1-5.—1. *Pseudanophthalmus t. tenuis* (Horn), King's Cave, Harrison Co., Indiana; transfer apparatus of male genitalia. Actual size, 0.30 x 0.14 mm. 2. *Pseudanophthalmus youngi donaldsoni* Krekeler, paratype, Donaldson's Cave complex, Lawrence Co., Indiana; transfer apparatus exserted from median lobe. Actual size, 0.57 x 0.14 mm. 3. *Pseudanophthalmus s. shilohensis* Krekeler, topotype, Shiloh Church Cave, Lawrence Co., Indiana; transfer apparatus, right dorsal and left ventral copulatory pieces slightly separated. Actual size, 0.29 x 0.14 mm. 4. *Pseudanophthalmus eremita* (Horn), topotype, Wyandotte Cave, Crawford Co., Indiana; aedeagus. 5. *Pseudanophthalmus leonae* n. sp., holotype male, Hert Hollow Cave, Lawrence Co., Indiana; aedeagus. (Scale of 0.5 mm for Figs. 4 and 5).

LEONAE GROUP

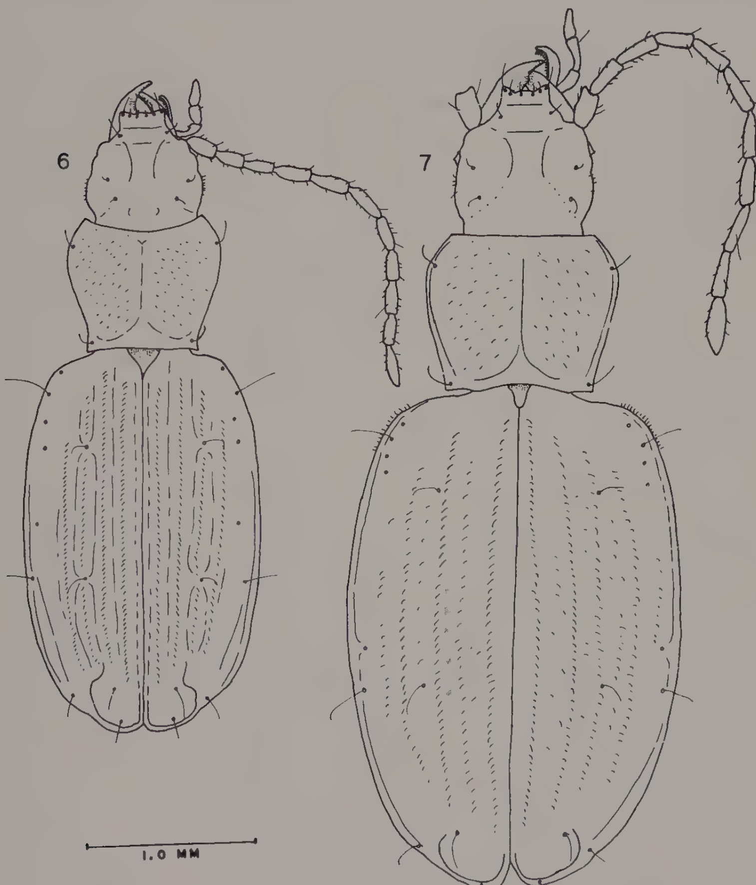
Size very small (3.2-3.8 mm). Head short and rounded, labrum trilobate. Pronotum transverse, pubescent, posterior angles quadrangular. Elytra oblong-oval, pubescent; humeri setose but not serrulate; first discal seta at level of fourth marginal puncture; chaetotaxial index high (0.67-0.68); apical recurrent stria rounded, bending sharply to the third longitudinal stria at the level of the third discal puncture. Aedeagus short and thick, basal flexure almost a right angle, apex blunt and truncate; basal keel small, subterminal; right copulatory piece large and broad (membranous?) in lateral view, triangular, apex hatchet-shaped; left piece narrower, a blunt rod (hollow or rolled?); internal sac armed with oblique rows of large scales; genital index 0.13. Type: *P. leonae* new species.

Pseudanophthalmus leonae new species.

Figs. 5, 6

Length 3.18-3.80, mean 3.58 mm. Color pale, rufo-testaceous.

Form robust and depressed. Head small and rounded; labrum doubly emarginate, the median lobe quite low but distinct. Pronotum transverse (index 1.19-1.23, mean 1.20), pubescent; anterior angles blunt; sides arcuate, basal sinus beginning about the basal third; posterior angles small, quadrangular; base very slightly concave to irregular. Elytra elongate-oval, depressed; disc with rows of pubescence; longitudinal striae very shallow but distinct, somewhat indented at punctures of first and second discal setae; first discal seta a little posterior to the level of the fourth marginal papilla; humeri rounded, setose but not serrulate; prehumeral border medium oblique to the midline; apical recurrent stria a wide arc running abruptly at its interior ter-



Figs. 6-7.—6. *Pseudanophthalmus leonae* n. sp., holotype male, Hert Hollow Cave, Lawrence Co., Indiana. 7. *Pseudanophthalmus eremita* (Horn), Langdon's Cave, Harrison Co., Indiana.

minus into the third longitudinal stria, in some specimens continuing to the second stria. Antennae scarcely reaching the middle of the elytra when laid back. Legs rather long. Aedeagus 0.51 mm long, small, short, and thick; transfer apparatus large (0.27 the length of the median lobe), left piece about three-fourths as long as right piece; parameres slender, bearing four long setae of unequal length.

Type series. Holotype male, allotype female, and two paratypes, Hert Hollow Cave, two miles SW. of Springville, Lawrence Co., Indiana, August 18 and 19, 1957, Catherine K. Barr and T. C. B. Holotype and allotype deposited in the American Museum of Natural History.

Holotype. Total length 3.78 mm, head 0.83 x 0.69 mm, pronotum 0.74 x 0.87 mm, elytra 2.16 x 1.32 mm, antennae 2.01 mm, aedeagus 0.51 mm.

Allotype. Total length 3.18 mm, head 0.78 x 0.60 mm, pronotum 0.60 x 0.74 mm, elytra 1.75 x 1.15 mm, antennae 2.01.

This tiny beetle is one of the smallest known species in the genus, comparable in size to *P. lallemanti* Jeannel (West Virginia). By its size alone it is immediately distinguished from all other described species of Indiana anophthalmids. Hert Hollow Cave is located at Sycamore Valley Farm, on the property of Miss Leona Hert, whose assistance and hospitality made possible the capture of this unusual beetle. The "cave" is only 30 feet long, 8 to 10 feet wide, and 5 feet high. Wooden steps descend to a small subterranean stream, along the edges of which, among small rocks and rootlets, the beetles were collected. A larger female *Pseudanophthalmus*, assigned to *P. s. shilohensis*, was also taken in Hert Hollow Cave. Since the cave floods and is much colder in winter and spring, it is probable that *P. leonae* can be taken in the type locality only during late summer and fall.

TENUIS GROUP

Pseudanophthalmus tenuis tenuis (Horn) new comb.

Anophthalmus tenuis Horn 1871: 327. Type: Wyandotte Cave, Crawford Co., Indiana (Acad. Nat. Sci. Philadelphia).

Anophthalmus eremita, Leng 1920: 55. Not of Horn 1871: 325.

Pseudanophthalmus eremita of various authors. Jeannel 1928: 131. Jeannel 1931: 466. Valentine 1932: 275. Jeannel 1949: 56. Krekeler 1958: 170.

Syn. *Pseudanophthalmus eremita longicollis* Jeannel 1949: 57. Type: Bradford Cave, Harrison (not Crawford) Co., Indiana (Mus. Nat. Hist. Nat. Paris).

Syn. *Pseudanophthalmus bloomi* Krekeler 1958: 172. Type: Langdon's Cave, Harrison Co., Indiana (Chicago Nat. Hist. Mus.).

P. t. tenuis was collected in eight caves, as follows: (1) Wyandotte Cave, Crawford Co.—33 specimens (July, 1957, and October, 1958, L. D. Lamon, L. D. Lamon, Jr., T. C. B.). (2) Seibert's Well Cave, Crawford Co., ¼ mile S. of Wyandotte Cave—one female (October, 1958, T. C. B.). (3) Langdon's Cave, Harrison Co., 2.4 miles SE. of Wyandotte Cave — 7 specimens (July, 1957, and October, 1958, T. C. B.). (3) Langdon's Cave, Harrison Co., 2.4 miles SE. of Wyandotte Cave — 7 specimens (July, 1957, and October, 1958, T. C. B.). (4) King's Cave, Harrison Co., 3.5 miles SE. of Corydon — 18

specimens (July, 1957, T. C. B.). (5) Binkley's Cave, Harrison Co., one mile S. of Corydon—78 specimens (August, 1957, Catherine K. Barr, T. C. B.). (6) Bradford (Steerstetter) Cave, Harrison Co., 0.5 mile E. of Bradford on the left bank of Corn Creek—33 specimens (August, 1957, Leslie Hubricht and T. C. B.). This is the Bradford Cave described by A. S. Packard (1888) who wrote that anophthalmid beetles were more abundant here than in any other cave he had visited. (7) Sweet Potato Cave, Harrison Co., 0.6 mile N. of Byrneville on the right bank of Corn Creek—one male and two females (August, 1957, T. C. B.). (8) Goss Cave, Washington Co., two miles SW. of Martinsburg—17 specimens (August, 1957, L. D. Lamon and T. C. B.).

Variations in six populations of *P. t. tenuis* are presented in Table I. No consistent qualitative variations were discovered. The meristic data obtained indicate a modicum of local variation but do not justify subspecific differentiation from the Wyandotte population. "Total length" was measured in millimeters, from the tips of the mandibles to the apices of the elytra. The "pronotal index" is the greatest width of the pronotum divided by the length measured along the midline. The "chaetotaxial index," as defined by Valentine (1945), is the dis-

TABLE I.—Meristic variations in different cave populations of *Pseudanophthalmus t. tenuis* (Horn)[1]

Cave	No. Specimens	Total Length	Pronotal Index	Chaetotaxial Index
Wyandotte	30	5.12 ± 0.06	1.07 ± 0.01	0.46 ± 0.01
Langdon's	7	4.90 ± 0.14	1.12 ± 0.03	0.46 ± 0.01
King's	18	5.00 ± 0.05	1.09 ± 0.01	0.49 ± 0.01
Binkley's	20	5.21 ± 0.02	1.07 ± 0.01	0.46 ± 0.01
Bradford	20	4.84 ± 0.06	1.11 ± 0.01	0.48 ± 0.01
Goss	17	5.02 ± 0.08	1.09 ± 0.01	0.46 ± 0.01
		No. Aedeagi	Aedeagus Length	
Wyandotte	30	5	0.81 ± 0.02	
Langdon's	7	4	0.83 ± 0.01	
King's	18	5	0.83 ± 0.02	
Binkley's	20	5	0.82 ± 0.01	
Bradford	20	6	0.80 ± 0.01	
Goss	17	5	0.83 ± 0.01	

[1] All lengths in millimeters.

tance between the first and fourth marginal elytral punctures divided by the distance between the fourth and fifth punctures, and indicates the degree of spacing of the humeral set of four prominent setae.

The distinguishing characteristics of *longicollis* (Jeannel, 1949) were said to be (a) pronotum longer than wide, and (b) apex of aedeagus more attenuate. With a pronotal index which averages 1.11, the Bradford Cave population as a whole is quite different from what Jeannel's two cotypes led him to believe. Of the six aedeagi examined, two were slender and attenuate, but the other four were indistinguishable from typical Wyandotte *tenuis*.

In his diagnosis of *bloomi*, Krekeler (1958) lists four criteria for distinguishing *bloomi* from the Wyandotte population: (a) size smaller, (b) chaetotaxial index higher, (c) apical stria curved, not sinuate or parallel to the suture, and (d) left copulatory piece not subapically constricted and deflected. As indicated in Table I, the mean length of the writer's series from Wyandotte is 5.12 ± 0.06, whereas Krekeler's series averaged 5.32 ± 0.07, a difference probably attributable to sampling error. The average lengths of Krekeler's and the writer's series of beetles from Langdon's Cave are 4.80 ± 0.12 and 4.90 ± 0.14, respectively. Table I shows identical means (0.46 ± 0.01) for chaetotaxial indices in the writer's samples from both caves. The apical recurrent stria appears singularly unreliable in both Wyandotte and Langdon's populations. In the writer's seven Langdon's specimens the recurrent portion of the stria may be (a) arcuate, with three variations; (b) subparallel to the suture; (c) flared laterally to connect with the 5th longitudinal stria; or (d) weakly sinuate. Similar variations obtain among Wyandotte beetles.

The structure of the *tenuis* transfer apparatus has proved difficult to interpret in whole mounts of aedeagi. Jeannel (1931) confused the right and left pieces, and as he himself admitted, his earlier representation of this structure (1928) was wholly inaccurate. In *tenuis, shilohensis,* and *youngi* the writer found it necessary to dissect the transfer apparatus from the median lobe in order to determine its structure. In the following description of the *tenuis* apparatus (Fig. 1) both Krekeler (pers. comm., April 2, 1959) and the writer are essentially in agreement.

The right piece, a large membrane supported at the base by a sclerotized thickening, is flexible and varies slightly in length in any preparation. It is medially concave and partially envelops the left piece; in lateral view it appears dorsally concave. The apex bears a fine, irregular hook dorsally, with a notch below. The left piece is a rolled half tube, open medially along its length, with thickened walls and spiny armature. It has the shape of a tall cone, tapering apically and terminating in an ellipsoidal, translucent plate. The "normal" position of this terminal plate is presumably vertical, but in the preparation of slides it may rotate as much as 120°, varying in appearance with the angle at which it is viewed. In the examination of about 35 aedeagi of *tenuis,* no left piece was encountered which was

constricted subapically, though the variable degree of rotation presents several aspects in lateral view.

The known range of *P. t. tenuis* is roughly triangular, about twelve miles broad at the base and about eighteen miles along each of the other two sides. This beetle is thus an abundant, highly variable, wide-ranging form similar in distribution and variation to *P. menetriesi* (Motschulsky) and *P. r. robustus* Valentine (Kentucky and Tennessee species, respectively). Additional collecting, especially in southwestern Harrison County, may possibly increase the number of localities for this subspecies.

Pseudanophthalmus tenuis stricticollis Jeannel

Pseudanophthalmus eremita stricticollis Jeannel 1931:45. Type: Marengo Cave, Crawford Co., Indiana (Mus. Nat. Hist. Nat. Paris).
Pseudanophthalmus stricticollis, Krekeler 1958:170.

This subspecies is known only from Marengo Cave, twelve miles N. of Wyandotte Cave (C. Bolivar, R. Jeannel, H. Morrison, 1928; C. H. Krekeler, 1950; L. D. Lamon, Catherine K. Barr, T. C. B., 1957). The longer antennae, larger size, lower chaetotaxial index, and larger aedeagus easily distinguish *stricticollis* from nominate *tenuis* (cf. Jeannel, 1931; Krekeler, 1958).

Pseudanophthalmus tenuis jeanneli Krekeler

Pseudanophthalmus jeanneli Krekeler 1958:171. Type: Elrods Cave, Orange Co., Indiana (Chicago Nat. Hist. Mus.).

P. t. jeanneli is known only from five specimens taken in Elrod's Cave, which opens at the edge of Wesley Chapel Gulf (C. H. Krekeler and W. W. Bloom, 1950; Catherine K. Barr, T. C. B., 1957). The average length for the five specimens is 5.34 ± 0.21 mm, the pronotal and chaetotaxial indices for four are 1.09 ± 0.06 and 0.46 ± 0.03, respectively, and the three aedeagi measure 0.88, 0.94, and 0.96 mm. This subspecies may be distinguished from most of the other subspecies of *tenuis* by its larger aedeagus and longer antennae (index 0.65-0.71, av. 0.67), and from *stricticollis* by the shorter recurved portion of the apical stria.

Pseudanophthalmus tenuis morrisoni Jeannel

Pseudanophthalmus eremita Morrisoni Jeannel 1931:451. Valentine 1932: 275. Jeannel 1949:56. Type: Donaldson Cave, Lawrence Co., Indiana (Mus. Nat. Hist. Nat. Paris).
Pseudanophthalmus morrisoni, Krekeler, 1958:171.

This subspecies is readily distinguished by its larger size, greater aedeagal length, and the unusually wide pronotum. It is known only from the Donaldson Cave complex in Spring Mill State Park (R. Jeannel, C. Bolívar, H. Morrison, 1928; C. H. Krekeler, 1950; T. L. Poulson, 1957; T. C. B., 1957).

Pseudanophthalmus tenuis blatchleyi new subspecies
Fig. 8

Type. A unique male from Truitt's Cave, near Bloomington, Monroe Co., Indiana, U. S. National Museum, acquired as part of the Wickham collection. Collection data other than locality unknown. Female unknown.

Length 5.90 mm. Head unusually wide (1.29 x 1.01 mm, index 0.79). Pronotum normal (1.10 x 1.19 mm, index 1.08), posterior angles a little smaller and less produced. Elytra 3.26 x 1.93 mm, index 0.59; chaetotaxial index 0.42; apical recurrent stria short and rounded on left elytron, turning somewhat abruptly inward at its anterior terminus on the right elytron, running into third longitudinal stria. Antenna 4.02 mm, index 0.68. Aedeagus (Fig. 8) 1.03 mm, large and thick, apex somewhat truncate; copulatory pieces subequal in length; parameres bearing five setae.

P. t. blatchleyi is distinguished from most subspecies of *tenuis* by its greater total length and aedeagal length. From *morrisoni* — a subspecies comparable in both of these characters — it differs in the narrower pronotum and larger, wider head. From *P. shilohensis mayfieldensis,* which inhabits the same cave, it is readily distinguished by the larger size, wider head, less sharply defined median lobe of the labrum, reduced hind angles of the pronotum, apical recurrent stria running to the third and not to the fifth longitudinal elytral stria, and the transfer apparatus.

This subspecies is unfortunately known only from the type. During removal of the aedeagus the apex of the median lobe was accidentally broken off, and the accompanying drawing (Fig. 8) is consequently a reconstruction from the two pieces. This circumstance, however, afforded an excellent view of the transfer apparatus. It is to be hoped that future collections will yield additional specimens and permit an adequate description of the range of variation in *blatchleyi.* The writer is not completely satisfied that *morrisoni* and *blatchleyi* contribute to the same gene pool as *tenuis* s. str., *stricticollis,* and *jeanneli,* but would prefer to have more evidence of genetic isolation before elevating them to full species.

This subspecies is named in honor of W. S. Blatchley, a pioneer in

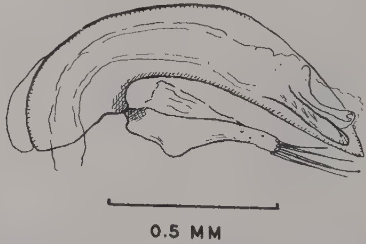


Fig. 8.—*Pseudanophthalmus tenuis blatchleyi* n. subsp. Type, Truitt's Cave, Monroe Co., Indiana; aedeagus.

the investigation of Indiana caves and their fauna and a widely known student of Indiana beetles.

YOUNGI GROUP

Pseudanophthalmus youngi youngi Krekeler

Pseudanophthalmus youngi Krekeler 1958:175. Clifty Caves, Washington Co., Indiana (Chicago Nat. Hist. Mus.).

Known only from the type locality, located four miles N. of Campbellsburg (C. H. Krekeler, 1950; T. C. B., 1957).

Pseudanophthalmus youngi donaldsoni Krekeler
Fig. 2

Pseudanophthalmus donaldsoni Krekeler 1958:175. Type: Donaldson Cave complex, Lawrence Co., Indiana (Chicago Nat. Hist. Mus.).

Known only from the type locality, Donaldson, Bronson, and Upper and Lower Twin Caves, in Spring Mill State Park (C. H. Krekeler, 1950, 1953; T. L. Poulson, 1957, 1958). The four caves have been connected by direct exploration. The Donaldson population differs in minor respects from the Clifty population, eight miles distant. The differences cited by Krekeler (1958) were found relatively consistent in the writer's samples from both caves.

The transfer apparatus of *youngi* (Fig. 2) is one of the most complex within the genus. The left dorsal copulatory piece is a somewhat flattened rod, the left edge of which is heavily sclerotized and folded. The right ventral piece forms about two-thirds of a tube beneath the left piece; the apex is shaped like the bow of a canoe, a small hamulate process extending slightly beyond the apex of the left piece.

SHILOHENSIS GROUP

Pseudanophthalmus shilohensis shilohensis Krekeler
Fig. 3

Pseudanophthalmus shilohensis Krekeler 1958:178. Type: Shiloh Church Cave, Lawrence Co., Indiana (Chicago Nat. Hist. Mus.).

P. s. shilohensis is known from three caves in Lawrence County: Shiloh Church Cave, near Eureka Springs (C. H. Krekeler, 1949, 1950; Catherine K. Barr and T. C. B., 1957); Donnehue's Cave, a mile S. of Bedford (T. C. B., 1957); and Hert Hollow Cave, two miles SW. of Springville (one female, T. C. B., 1957). The specimen from Hert Hollow Cave is tentatively referred to this subspecies until males can be collected.

The transfer apparatus of *shilohensis* (Fig. 3) is diagnostic, though its position within the median lobe renders it difficult, if not impossible, to interpret in whole mounts of the aedeagus. It consists of left dorsal and right ventral copulatory pieces, both spatulate and ventrally concave, the left dorsal piece smaller and nested within the right ventral piece, forming a wide spout.

Pseudanophthalmus shilohensis mayfieldensis Krekeler

Pseudanophthalmus mayfieldensis Krekeler 1958:178. Type: Mayfield's Cave, Monroe Co., Indiana (Chicago Nat. Hist. Mus.).

P. s. mayfieldensis inhabits the caves of Monroe County in the vicinity of Bloomington. The type locality, Mayfield's Cave, was studied extensively in the classic investigations of Banta (1907), who stated that this beetle (determined as "Anophthalmus tenuis") was "fairly common" but "not abundant." Ten specimens were collected crawling about among cobbles, beneath which flowed a very shallow branch of the cave stream (August, 1957, Heiner Hoffman and T. C. B.). One male was collected in May's Cave, Monroe County (August, 1957, T. C. B.). Specimens from Truitt's Cave, Monroe County, were examined in the U. S. National Museum collection, and are referred to *P. s. mayfieldensis.* This subspecies differs from *P. s. shilohensis* principally in the wider pronotum and in having usually three (four in *shilohensis*) setae on the parameres. The apical recurrent stria may be connected directly with the third longitudinal stria or flared laterally toward the fifth stria, though aedeagi of both variants are indistinguishable. Only the latter strial condition obtains in the writer's series of eighteen *P. s. shilohensis.*

Pseudanophthalmus shilohensis boonensis Krekeler

Pseudanophthalmus boonensis Krekeler 1958:180. Type: Boone's Cave, Owen Co., Indiana (Chicago Nat. Hist. Mus.).

P. s. boonensis has been collected only in Boone's Cave, a mile N. of Freeman (C. H. Krekeler, 1950; T. C. Barr, 1957, one female). The type series consists of only three specimens. The type cave is behind the terminal moraine of the Illinois glacier, indicating that this beetle colonized its present habitat no earlier than Sangamon time.

Discussion

Externally, *tenuis, shilohensis,* and *youngi* share several features suggestive of close relationship: (a) elongate, rather convex body and slender appendages; (b) median lobe of labrum prominent; (c) pronotum narrowed in basal third, posterior angles acute and produced beyond the base; (d) shallow longitudinal striae on the elytra; and (e) short, usually rounded apical recurrent striae, running alternately to the third or the fifth longitudinal stria. All have a slender, strongly arcuate aedeagus, the apex of which is usually only briefly attenuate. The greatest divergence occurs in the transfer apparatus. Even here the similarities are striking — the right piece is a large, medially concave membrane, strongly sclerotized at the base, partially enveloping the smaller left piece. This relationship is rendered clear by studying the transfer apparatus apart from the median lobe, and in *youngi* and *shilohensis,* allowing for a 90° rotation from the normal position as

found in *tenuis*. A close common ancestry for all three species is indicated.

The *eremita* group seems most closely related to the *robustus* group of *Pseudanophthalmus,* species of which inhabit caves of the Eastern Highland Rim and the western margin of the Cumberland Plateau in Tennessee and southern Kentucky. It resembles *robustus* itself in the robust, depressed form; the position of the first discal seta; the large, rounded, apical stria; and especially in the shape of the aedeagus and the nature of the transfer apparatus. It differs in the virtual absence of longitudinal elytral striation; the slightly greater development of pubescence; and the close spacing of the humeral marginal setae. There are also minor but possibly significant differences in the shape of the apical stria and in the relative lengths and sizes of the copulatory pieces.

A nearer relationship geographically, if somewhat more distant morphologically, is perhaps to be sought in *Pseudanophthalmus* of the *menetriesi* group, which possess an elongate, flattened right copulatory piece with thickened edges, and a rod-like left piece the apex of which is slightly enlarged. Specimens unquestionably related to *P. menetriesi* have been collected from Hardin County, Kentucky, southward and eastward to Clay County, Tennessee.

P. leonae appears to be an intermediate form in some measure uniting the major characteristics of both the *tenuis-shilohensis-youngi* aedeagus and that of the *eremita-robustus-menetriesi* line. In the robust, depressed body form, the low median lobe of the labrum, and the shape of the pronotum, *leonae* resembles *eremita* and *emersoni,* but the lamellar (probably membranous) right copulatory piece and the small, rod-like left piece bespeak a distant tie with *tenuis.*

The great variety of genital types of *Pseudanophthalmus* within a small area is a striking characteristic of the Mitchell plain assemblage. Five species groups are compressed into a region 100 miles long by 25 miles wide. This variety attains a maximum in Lawrence County, toward the northern terminus of the region, where all five groups are present. For a possible explanation of this phenomenon one may consider the factors influencing cave colonization by trechine beetles. Jeannel (1949) suggested that the cool, moist glacial climates favored the geographic expansion of the trechines, and that environmental conditions were most favorable at the very periphery of the ice sheets. During the warmer, drier interglacials the trechines retreated to the summits of the Appalachians, to the north, or into caves. Although we could expect cave colonization by these beetles in any major limestone area climatologically affected by the ice sheets, it seems probable that the greatest diversity of surface species would occur near the edge of the ice, and that in such regions the possibility for colonization of caves by a maximum number of species would be greatest. In eastern North America the Mitchell plain — a northward extension of the great cave region of Kentucky, Tennessee, and Alabama — is the only major cave area bordering a terminal moraine of a Pleistocene ice sheet, and would have afforded numerous caves for colonization

by cryptozoic beetles. It is suggested that the Mitchell plain species of *Pseudanophthalmus* represent the remnants of a rich periglacial fauna, and that their diversity is the direct result of the optimum environmental conditions which prevailed at the margins of the Illinois and/or Wisconsin ice sheets.

If this hypothesis be correct, we may expect the discovery of additional new and unusual trechines in caves of the Mitchell plain. It would not be surprising if these forms prove to be quite rare or limited in distribution, like *eremita, emersoni,* and *leonae.* If their ecological niches do not in fact coincide with those of abundant, wide-ranging species like *P. tenuis* and *P. shilohensis,* there must at least be considerable overlap, resulting in intense competition with apparently more successful species. This interpretation suggests as its corollary that the rare, localized species (*eremita, emersoni,* and *leonae*) are moribund stocks close to extinction.

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Alteration of the Composition of Rainwater by Trees

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During a study of the distribution of rainfall on the forest floor (Voigt, 1959) it was observed that tree canopies are subject to considerable leaching by rainwater. This water ultimately reaches the soil by dripping from the foliage and small branches or it is concentrated by the branches and funneled down the stem. The former component is generally termed throughfall and the latter is designated as stemflow. Although previous studies (Stenlid 1958; Tamm, 1951; 1953) have shown that salts are removed from tree canopies by rainfall, none of these authors has considered the contribution of stemflow to this segment of the nutrient cycle. Pozdnyskov (1956) determined acidity, dry matter content and ash content of stemflow water from birch, larch and pine, but no detailed chemical analyses were given. The present investigation was concerned with the nutrient content of rainwater, its modification by three forest cover types, and with the net nutrient return to forest soils resulting from the addition of rainwater.

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Methods and Materials

The study area was located in southern Connecticut about eight miles east of New Haven. This area receives about 45 inches of precipitation per year, mostly as rain. Water samples were collected from two storms; one in May and one in September from four cover types: red pine (*Pinus resinosa*, Ait.), hemlock (*Tsuga canadensis* [L.] Carr.), beech (*Fagus grandifolia*, Ehrh.) and an open area. The plots were arranged along a line which measured roughly a quarter of a mile from one extreme to the other. Stemflow samples were collected from seven trees in each forest cover type and throughfall samples were collected in five rain gauges scattered on each forested plot. Total rainfall for each storm was determined by five rain gauges near the center of the open area. The latter samples were also used to determine the initial composition of rainwater. The May storm totaled 0.97 inches and the September storm totaled 1.01 inches.

Total nitrogen content of the water was determined by the Kjeldahl method within a day after collection. Nitrate nitrogen was determined by the phenoldisulfonic procedure, but since the water samples showed virtually no nitrate nitrogen, the values in Table I refer to the results of determination of Kjeldahl nitrogen which includes organic and ammonium forms. Potassium and calcium were measured with a Beckman DU flame spectrophotometer. Phosphorus

was determined colorimetrically, using the ammonium molybdate-stannous chloride method. Potassium, calcium and phosphorus determinations were made on acidified samples that had been concentrated by evaporation (Wilde and Voigt, 1959).

Results and Discussion

The composition of rainwater modified by tree canopies is compared with natural rainwater in Table I. The values for natural rainfall tend to be slightly higher than those reported previously (Tamm, 1951; 1953). Both this fact and the differences in contents of K and Ca in May and September are probably related to the close proximity of the study area to the highly industrial region of the eastern seaboard. Differences in direction of storm movement or prevailing surface winds could conceivably cause great differences in the amount of air pollution.

Table I.—Composition of rainwater collected under different forest cover types

COVER TYPE	MAY N ppm	MAY P ppm	MAY K ppm	MAY Ca ppm	SEPTEMBER N ppm	SEPTEMBER P ppm	SEPTEMBER K ppm	SEPTEMBER Ca ppm
Open area	0.05	0.01	0.3	0.6	0.07	0.01	0.6	0.8
Red Pine								
Throughfall	0.05	0.04	0.6	1.7	0.05	0.04	1.7	1.5
Stemflow	0.12	0.07	7.2	2.2	0.18	0.08	6.5	15.3
Hemlock								
Throughfall	0.03	0.03	0.6	1.9	0.08	0.03	2.7	2.2
Stemflow	0.10	0.05	0.8	3.0	0.11	0.08	6.3	7.8
Beech								
Throughfall	0.05	0.03	0.5	1.1	0.09	0.04	1.7	1.5
Stemflow	0.04	0.04	0.6	1.1	0.16	0.06	6.1	1.5

It is possible that industrial contamination also contributed to the values shown for water collected under forest cover. However, both collection dates were preceded by one or more days of precipitation so that most of the dust particles from the atmosphere that had settled on the leaf surfaces had been removed. Thus, it appears that the modification in rainwater composition resulted from addition or removal of ions by the trees. Since the first sampling period corresponded roughly to the initial burst of growth and the second one to the onset of dormancy, it would appear also that the observed differences were related to seasonal variations in metabolic activity and changes in the anatomical characteristics of the leaves.

Within each sampling period the composition of the water collected as stemflow showed greater species differences than the water collected beneath the tree canopies. These differences are probably related to variations in bark texture among the species observed. Red

TABLE II.—Movement of nutrients in rainwater under different forest cover types

COVER TYPE	MAY				SEPTEMBER			
	N mgm	P mgm	K mgm	Ca mgm	N mgm	P mgm	K mgm	Ca mgm
Open area								
Addition to soil/acre*	5	1	30	59	6	1	59	72
Red pine								
Throughfall/tree	6.0	4.8	72.2	204.6	6.1	4.8	204.6	180.6
Stemflow/tree	0.3	0.1	17.3	5.3	0.4	0.2	15.6	36.7
Return to soil/tree	6.3	4.9	89.5	209.9	6.5	5.0	220.2	217.3
Return to soil/acre*	3	3	45	105	3	3	110	109
Tree contribution/acre*	–2	+2	+15	+44	–3	+2	+51	+37
Hemlock								
Throughfall/tree	5.1	5.1	101.4	321.2	13.7	5.0	456.5	372.0
Stemflow/tree	1.3	0.6	10.7	40.2	1.5	1.1	84.4	93.6
Return to soil/tree	6.4	5.7	112.1	361.4	15.2	6.1	540.9	465.6
Return to soil/acre*	3	3	52	166	7	3	249	214
Tree contribution/acre*	–2	+2	+22	+97	+1	+2	+190	+142
Beech								
Throughfall/tree	13.3	8.0	133.9	294.5	24.1	10.7	455.2	401.7
Stemflow/tree	1.2	1.2	18.0	33.0	4.8	1.8	183.0	45.0
Return to soil/tree	14.5	9.2	151.9	327.5	28.9	12.5	638.2	446.7
Return to soil/acre*	5	3	49	105	9	4	204	143
Tree contribution/acre*	0	+2	+19	+44	+3	+3	+145	+71

* Values are in grams

pine and hemlock have rough bark and hence more surface area than beech on which the bark is smooth. Presumably the rough bark would also be subject to more contamination from mosses, lichens and other organisms.

The study of rainfall distribution referred to earlier (Voigt, 1959) allowed calculation of the magnitude of salt movement to show the net return to the soil under the three forest cover types studied. These data which are presented in Table II were obtained by relating the composition values from Table I to the mean amounts of water added as throughfall or stemflow under a single tree of each species. These figures were converted to the acre basis by multiplying by the appropriate number of trees per acre. It is apparent that the higher nutrient concentration in stemflow shown in Table I was outweighed by the greater amount of water added as throughfall. Therefore, water dripping through the canopy constituted a substantially greater proportion of the net soil addition than did stemflow.

Comparison of the amounts of nutrients added by rainwater to soil in the open with the return under forest trees indicates that the trees made a substantial contribution to the soil in nearly all cases. The exception to this generality was nitrogen. The returns per acre in May under red pine and hemlock and the September values for red pine were lower than the addition to the soil in the open. Apparently the foliage of the trees absorbed nitrogen from the rainwater instead of releasing it. This phenomenon was also observed by Tamm (1951), but his values referred to rainwater concentrations rather than net soil returns. The only instance in which significant amounts of nitrogen were released by the trees occurred in the samples collected under beech in September.

The values for potassium and calcium were generally higher in September than in May. The increased amounts of salts added to the soil in the open offer a partial explanation. It seems reasonable, however, that changes in the nutrient requirements accompanying the approach of dormancy are also involved. Potassium in these trees was more vulnerable to extraction by rainwater in September than in May. It is also apparent that potassium was more easily extracted than calcium in September whereas the reverse was true in May. Leaching of calcium from red pine showed a relative decrease in September, but in hemlock and beech more calcium was extracted at the end of the growing season. Although the September samples were collected well in advance of autumnal color changes, it is likely that the abscission layer had already begun to form in the beech leaves. Thus, the leaf would be essentially isolated from the tree and any nutrient transfer from leaf to tree would be reduced to a minimum. Red pine and hemlock retain their needles for three or more years so that ample opportunity would exist for nutrient transfer associated with dormancy. The observed variations in these three species undoubtedly reflect fundamental differences in their physiological processes. Superimposed on these differences was the vari-

ability which may have existed in the chemical composition of the soil.

The values in Table II are based on two storms and hence do not allow a precise estimate of total nutrient movement. It is reasonable to expect, however, that a mean value for each cover type would fall within the range indicated by the two extremes of the growing season. If one uses this assumption and an average rainfall figure of 19 inches for the growing season in Connecticut (U.S.D.A., 1941, Climate for Connecticut), approximations are obtained which indicate that the return of nitrogen and phosphorus in rainwater is of little importance. The return of potassium ranges from about two to ten pounds per acre and calcium ranges from six to nine pounds per acre during the growing season. It is likely that under species with foliage high in mineral nutrients, such as tulip poplar (*Liriodendron tulipifera,* L.), basswood (*Tilia americana,* L.), hackberry (*Celtis occidentalis,* L.) and flowering dogwood (*Cornus florida,* L.) considerably more potassium and calcium is returned to the soil (Lutz and Chandler, 1946).

It should be emphasized that these nutrient movements from the tree to the soil do not constitute independent additions to the nutrient capital. They are merely segments of the nutrient cycle which may be recirculated from the soil to the tree and back to the soil several times during the growing season. Thus, it would be misleading to conclude that from two to ten pounds of potassium and from six to nine pounds of calcium per acre are added to the soils each growing season under red pine, hemlock, or beech. Instead these figures give an indication of the extent of nutrient circulation within the soil-tree system.

SUMMARY

The contents of nitrogen, phosphorus, potassium, and calcium were determined in rainwater collected under red pine, hemlock, and beech stands, and in an open area. Throughfall and stemflow samples were taken at the beginning and end of the growing season. The results showed that the composition of the water was altered by the trees and that the degree of alteration was affected by season, species, and location of collection with respect to the tree. The nutrient contents of water collected in September were higher than in samples collected in May. Stemflow from red pine and hemlock contained more nutrient elements than did stemflow from beech. Values for nutrient content of throughfall showed practically no correlation with species and were generally lower than values for stemflow. Calculation of nutrient movement indicated that considerable amounts of potassium and calcium were extracted from the foliage and branches and returned to the forest soils. Nitrogen and phosphorus returns were about the same as those received by the soil in the open area. It is felt that an approximation of the magnitude of the annual nutrient

circulation may be obtained by extending the data from the two storms observed.

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Sex Ratios and Population Density in Hibernating Myotis

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This study was undertaken as a part of an investigation of the biology, parasites and migration of bats of northwestern Texas supported by the National Institute of Health through a grant to Dr. Russell W. Strandtmann of Texas Technological College. We wish to acknowledge the help of many Texas Technological College faculty and students, but we are particularly indebted to Russell Strandtmann, Jessie Hillman, Colene Amondson, Chester Rowell and John E. George. We wish to thank Messrs. J. A. Hedgecoke of Amarillo, R. W. Walkup of Lazare and F. L. Richardson of Quanah for permission to study caves located on their ranches.

The data reported here were obtained in 1958 and 1959 in three gypsum caverns located in Armstrong, Cottle and Hardeman Counties in the Texas Panhandle. These caves lie within the mesquite plains and short grass plains of the Kansas biotic province (Blair, 1954). The major objectives of the investigation were to estimate population density in bats by mark and recapture techniques and to study sex ratios to determine if they fitted the general pattern suggested by previous authors. A total of 3288 *Myotis velifer incautus* were banded during the course of this study, most of them at three caves. Exact locality data on these and other distributional records have been reported (Milstead and Tinkle, 1959).

Sex Ratio

PANTHER CAVE

This cave is located on the Floyd Richardson ranch, 22 miles southeast of Childress, Cottle County, Texas. The cave was visited on six occasions between February 15, 1958, and March 6, 1959, when large numbers of bats were present (Table I). The figures in-

TABLE I.—Variation in the sex ratio of *Myotis* at Panther Cave

Date	Total bats	% ♂♂	% ♀♀
15 Feb. 1958	143	31	69
29 March 1958	208	38	62
26 April 1958	16	63	37
14 Nov. 1958	264	55	45
8 Feb. 1959	346	32	68
6 March 1959	30	30	70

cluded both banded and unbanded bats. On one occasion when a large number (123) banded bats were recovered, the sex ratio in the banded bats was about the same as that in the unbanded ones.

There is a clear-cut decrease in the percentage of males and increase in percentage of females during the winter. The figures for the same months in two different years are nearly the same.

WALKUP CAVE

This cave, located in the R. W. Walkup ranch, 3 miles southeast of Lazare in Hardeman County, Texas, is about two miles east of Panther Cave. Considerable exchange of bats occurs between the two caves. On five visits to this cave, large numbers of bats were encountered and the sex ratio of these samples shows a clear increase in the percentage of females and a decrease in that of males (Table II).

The sex ratio of banded bats was about the same as that of the unbanded ones when sufficiently large numbers of banded bats were recovered.

SINKHOLE CAVE

This cave, located on the Hedgecoks ranch, 29 miles southwest of Claude, Armstrong County, Texas, is 100 miles northeast of the other caves and no interchange between this and the other two caves has been noted.

Large numbers of bats have been found in this cave on seven occasions and the sex ratio of these shows a decrease in males and an increase in females although not as sharply as in the other two caves (Table III).

The sex ratio of banded bats which were frequently obtained in large numbers at this cave show the same general seasonal increase in females and decrease in males.

DISCUSSION

The disparity in sex ratio in bats at various seasons is known to be extreme. Hitchcock (1950) noted an apparent decrease in the percentages of males of several species the farther south one goes, although he did find a high percentage of male *Myotis lucifugus* (65.5%) in a cave in Kentucky. Since the sex ratio is known to be

TABLE II.—Variation in the sex ratio of *Myotis* at Walkup Cave

Date	Total bats	% ♂♂	% ♀♀
18 Oct. 1958	92	61	39
8 Nov. 1958	697	42	58
5 Dec. 1958	321	43	57
7 Feb. 1959	246	37	63
6 March 1959	209	31	69

TABLE III.—Variation in the sex ratio of *Myotis* from Sinkhole Cave

Date	Total bats	% ♂♂	% ♀♀
16 Feb. 1958	129	35	65
15 Nov. 1958	117	56	44
21 Nov. 1958	375	49	51
13 Dec. 1958	319	48	52
21 Feb. 1959	813	38	62
1 March 1959	118	40	60
21 March 1959	336	38	62

equal at birth, some other explanation of the disparity is necessitated. Rice (1957) in a study of *Myotis austroriparius* in Florida found that these bats show an increase in males in the spring and early summer and a decrease in the fall. Females always outnumbered males, however, by more than two to one. He examined data of this species presented by other authors and concluded, like Hitchcock, that the proportion of males was less in the south. Most authors (Hitchcock, *op. cit.;* Griffin, 1940; Mohr, 1945; Eisenstraut, 1947) report that populations of bats hibernating in caves contain a preponderance of males.

Davis (1959) studied disproportionate sex ratios in 4,000 hibernating *Pipistrellus subflavus* in 48 West Virginia caves and concluded that the percentage of females in the population increased as one went south. He suggested that the sex ratio may reflect the severity of the winter — the harsher the winter, the more males that overwinter in the cave. This accentuates the slightly greater female mortality and the tendency of females to winter outside the caves. His hypothesis would explain the extremely high percentage (over 90) of males reported in the far northern populations by Hitchcock (1950) and others where climatic conditions are more severe than in the south.

Rice (1957) in a study of *Myotis austroriparius* in Florida found that females always greatly outnumber males. His figures on sex ratio when compared with those on this same species from other areas show a decrease in the percentage of males from 71 percent in Indiana to 25 percent in Louisiana.

Eisenstraut (1947) banded 4890 *Myotis myotis* in Germany without noting the sex ratio and followed these bats as they returned to the cave in which they were banded for 11 years. His data on these banded bats show a preponderance of males for the first seven years, after which the sex ratios became equalized by the tenth year. He also found that the mortality rate of the females was higher than that of males.

Pearson, *et al.* (1952) found that the percentage of male *Corynorhinus rafinesquei* in California was higher in the sections of the state having a harsher winter. These data again suggest that climatic conditions may play an important role in regulating the sex ratio of cavern-dwelling bats.

Our data for three caves show clearly that the sex ratios are most nearly equal in the late fall, presumably when the bats are mating; after this period there is a steady decline in the percentage of males and an increase in females throughout the winter until the bats leave the caves in late winter and early spring. These data support the views of other authors in that the caves studied by us are in the southern United States in an area of moderate climatic conditions and contain a low percentage of males in the winter.

Several explanations for the change in sex ratio through the winter are possible:

1. Bats apparently arrive in the colony during the winter and are predominantly females. Griffin (1945) found that *Myotis* in New England moved about extensively from one cave to another during the winter months.

2. There is greater mortality among males than among females. We have no data as yet on mortality. Some studies of other bats have suggested slightly greater female mortality, others greater male mortality, with no very significant differences in any case, except possibly in *Myotis myotis* in Europe (Eisenstraut, 1947) in which female mortality was significantly greater than male.

3. A greater proportion of males than females emigrate during the winter for reasons of conditions within the caves or because of disturbance due to banding. How much this influences sex ratios can be determined by studying the sex ratio of bats that were banded at each cave, but never recovered, assuming that these bats left soon after their initial capture.

   These data show that of 302 bats banded at Sinkhole cave and never recovered, 137 (45%) were males. Of 211 not recovered at Panther Cave, 69 (33%) were males and of 616 not recovered at Walkup Cave, 293 (48%) were males. Clearly, there is not a greater number of male than female bats leaving the caves, so the disproportionment of sex ratios must be due to differential emigration or mortality within the cave.

It is of interest that Twente (1955a) showed that males of *Myotis velifer* were generally more abundant than females in the gypsum caverns he studied in south central Kansas and northwestern Oklahoma. The winters in that area are more severe and a greater percentage of males would be expected following the hypothesis of Davis (1959). Twente (*op. cit.*) also found, as we did, that sex ratios were more nearly equal in late October and November.

POPULATION DENSITY

Almost no published data on population density in bats are available. Those figures that have been published (Twente, 1955; Rice, 1957; Pearson, Koford and Pearson, 1952) are based on measurements of clusters and calculations of the number of bats per some unit of area.

Because it was felt that we were working with bat populations of a relatively small size, we were confident that mark and recapture data would give some idea of seasonal changes in population density. Two methods of density determinations were used. One of these was a Lincoln Index constructed as follows:

$$\frac{\text{No. of bats banded in precensus}}{\text{X (other bats present)}} = \frac{\text{No. of banded bats found in census}}{\text{No. of unbanded bats in census}}$$

$$\text{Population size} = \text{X} + \text{number banded in precensus}$$

The second method used was that of Hayne (1949) in which the population of any given time is based on the equation $P = \frac{\Sigma WX^2}{\Sigma WXY}$ in which W is the total number of marked and unmarked bats caught on each trip, X is the number previously marked and released and Y is the proportion of marked animals on each trip.

PANTHER CAVE

The mark and recapture data at Panther Cave are fewer than for the others. Only a few estimates can be made (Table IV).

Because Lincoln indices are based partly on succeeding figures while Hayne indices are based on preceding ones, one would expect the Lincoln Index of one trip to most closely match the Hayne Index for the next succeeding trip. The table shows a close approximation in the figures considering the above statement. There are too many gaps between trips for the data to be accurate unless little or no immigration or emigration occurred, but it is likely that considerable of both takes place.

TABLE IV.—Population estimation of *Myotis* in Panther Cave

Date	Lincoln	Hayne	Number seen	% of sample that was banded
15 Feb. 1958	1190	......	143	0
29 March 1958	......	1192	208	12
14 Nov. 1958	708	......	264	0
8 Feb. 1959	588	713	346	37
6 March 1959	......	736	34	59

TABLE V.—Population estimation of *Myotis* in Walkup Cave

Date	Lincoln	Hayne	No. of bats seen	% of sample that was banded
18 Oct. 1958	1173	------	92	0
8 Nov. 1958	1257	1137	697	8
5 Dec.. 1958	1350	1646	325	18
7 Feb. 1959	306	2107	245	24
6 March 1959	------	1886	209	44

WALKUP CAVE

The data on population density of *Myotis* in Walkup Cave are more extensive (Table V).

The actual numbers of bats seen indicated a buildup in population in the early winter and a steady decline thenceforth, but the indices do not indicate a decline in numbers until much later. The indices generally indicate bat numbers in the cave far exceeding what we have ever actually encountered. Since both of these indices will give high figures if there is a great deal of population turnover, this is taken as additional evidence that immigration and emigration of bats takes place throughout the winter.

SINKHOLE CAVE

All of the data on population densities of *Myotis* at this cave are from one winter, 1958-1959 (Table VI).

In this cave the figures based on Lincoln Index show a steady decline in numbers from late November while the Hayne Index shows a relatively steady increase. The actual number of bats found indicates a build-up in population until December and a decline thereafter. We were not always confident that every bat had been removed from the cave, but an intensive effort was made to do this on the last three trips and a fair degree of success is indicated by

TABLE VI.—Population estimation of *Myotis* in Sinkhole Cave

Date	Lincoln	Hayne	No. of bats seen	% of bats that had been banded
15 Nov. 1958	476	------	121	28
21 Nov. 1958	1654	483	399	18
13 Dec. 1958	1288	1639	891	24
21 Feb. 1959	1161	1797	825	27
1 March 1959	318	1707	197	71
21 March 1959	------	1839	338	62

the rapid increase of the percentage of banded from 27 percent on Feb. 21 to 71 percent on Mar. 1.

The fact that more bats and a smaller percentage of banded were found on March 21 than on March 1 is explained by assuming that bats are in the process of leaving the caves in the area and that a number of migratory transients stopped briefly at this cave en route to summer quarters which are as yet undiscovered.

For the first two estimates the figures for the two indices are very nearly the same, but after this there is an increasing disparity in the figures. In general the Lincoln Index figures are closer to the actual number of bats seen and since it is not based on cumulative figures it is probably more reliable than the Hayne Index which will be more greatly affected by emigration and immigration because it is based on cumulative figures.

If a cave were visited three days during one week and then left for several weeks and then again sampled for three days, the discrepancies in the figures that are due to emigration and immigration would be minimized and it is felt that reliable figures on seasonal variation in density could be obtained in this way. For this purpose the Lincoln Index may yield more reliable results.

SUMMARY

Sex ratios and population densities of *Myotis velifer incautus* in three hibernating cave colonies in northwest Texas were studied.

There is a near equal sex ratio only in the late fall or early winter presumably following mating. After this there is a steady decrease in the percentage of males and an increase in females. This is interpreted to mean there is a greater immigration of females than males into the colony throughout the winter. The percentage of males falls to about 30 percent in all three caves by the late winter and early spring when the bats leave all three caves.

Population densities were estimated by Lincoln and Hayne indices. The figures by the two methods were sometimes in close agreement, but were often widely disparate. Generally, the Hayne Index figures indicate population numbers which are felt to be too high on the basis of the actual number of bats encountered on each trip.

The Lincoln Index seems to yield more reasonable estimates, compared with the total number of banded and unbanded bats actually caught, and it is suggested that both estimates would be more accurate if the data were obtained on several successive days at a few periods of the year so that gaps between the precensus and census periods are greatly reduced.

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Seventeen New Species in the Genus Priocnessus (Hymenoptera: Psammocharidae) with Keys to Males and Females of All Known Neotropical Species

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There are at present only 6 known Nearctic species in *Priocnessus*. The genus has many more species in the Neotropics. Of the 17 new species described in this paper, 12 are based on females, 3 on males, and 2 on specimens of both sexes.[1] Twenty-seven species are represented in the keys given here for the Neotropical region.

The Genus Priocnessus Banks

Wings with long narrow marginal cell, with apex acute, about 0.5 its length from wing tips; 3rd cubital 1.3 to 1.5 longer than 2nd and wider, both much longer on cubitus than on marginal vein; basal vein basad of transverse by equal to or more than length of transverse; subdiscoidal in rear wings, barely interstitial to 4 or 5 times thickness of vein apicad of cubitus; clypeus raised above mouth parts, truncate or concave with a tooth in middle of front, about 2.0 as broad as long; interior orbits parallel or slightly converging at vertex; head slightly broader than long; pronotum very short on dorsal surface; metapostnotum almost always well evident, 0.3 to 0.5 as long as postscutellum; propodum not long, in a low curve, hardly any declivity; posterior tibiae of female with 2 rows of teeth on dorsal surface, broad, flat, thin, teeth (really rectangular plates) set crosswise of length, the ones on inner edge the larger; a spine about twice their length set just behind them and touching; the teeth in outer row smaller but often the spines almost as long; the teeth sloping backward and giving a concave appearance; the space between teeth covered with fairly long not dense hair; claws in female with a small sharp tooth about center of claw and a long sharp ray, last joint of posterior tarsi generally with a few spines on ventral surface, sometimes hardly evident; males with split teeth on claws, the inner generally short, and blunt, the outer ray sharp; some species have the posterior tibiae of the males with good spines and sometimes even small teeth.

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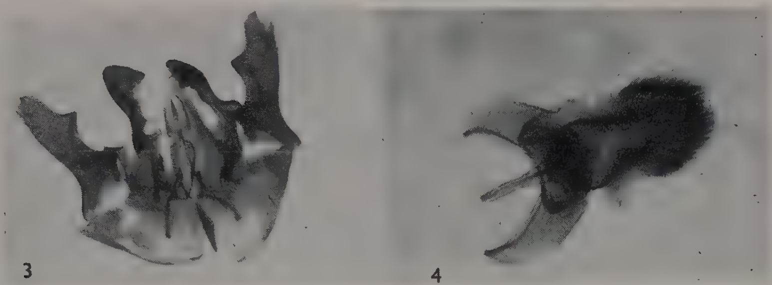
1 The designations for places of deposit of the type specimens in this paper are as follows: *MCZ* = Museum of Comparative Zoology, Harvard University; USNM = U.S. National Museum, Washington, D. C.; *RRD* = R. R. Dreisbach, Midland, Michigan; *Howden* = Dr. Henry F. Howden, Division of Entomology, Science Service, Ottawa, Canada; *Hurd* = Dr. Paul D. Hurd, Jr., Dept. of Entomology, University of California, Berkeley 4, California.

Priocnessus hondurensis n. sp.
Figs. 1, 2.

Holotype male.—Completely black over whole body, except apex of mandibles are reddish; head and thorax very hairy, hair very long from one-half to as long as the length of first two antennal joints; the abdomen with long hair on first tergite and at apex of last three, the ventral surface with a few long hairs on all sternites; head and thorax opaque, abdomen shining; from in front vertex even with top of eyes; head slightly longer than broad; interocular distance 0.6 the transfacial; width of vertex barely slightly longer than distance between eyes at clypeus; clypeus seven-twelfths as long as width; ocelli small in a small triangle, the lateral ones about three diameters from each other, and 3.5 as far from eyes as each other; antennae black, slender, and ratio of first four joints are as 15:8:28:28; clypeus almost truncate at apex and convex on sides, a shining rim on front extending around sides; the eyes reach the vertex; pronotum very short hardly any dorsal part, posterior edge arcuate; postnotum as long as postscutellum and transversly ridged; propodeum short and in a very low curve to apex; wings reddish, apex beyond cells blackish, and the rear edge blackish to base of third discoidal cell; marginal cell very long, its distance to wing tip one-fourth its length; about as wide as second cubital cell; second cubital cell longer than wide, as long on marginal vein as on base, receiving first recurrent vein at middle; third, cubital cell longer than the second, about two-thirds as long on marginal vein as on its base and receiving second recurrent vein before middle; basal vein basad of transverse vein by about the length of the latter; in the rear wings subdiscoidal vein is interstitial with the cubitus; claws split and the inner ray blunt, heavy, less than one-half length of the slender long sharp outer ray; longer spur of posterior tibiae more than one-half

Figs. 1 and 2.—*Priocnessus hondurensis* n. sp. 1.—Genitalia (x 15). 2.—Subgenital plate (x 30).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Figs. 3 and 4.—*Priocnessus octomaculatus* n. sp. 3.—Genitalia (x 30). 4.—Subgenital plate (x 30).

length of its metatarsal joint; genitalia with parameres well and long haired on the concave inside, longer than the other parts; volsellae with a large blunt hook or flange at apex on inside; parapenial lobes slightly longer than aedeagus; subgenital plate notched near middle on sides with a slightly elevated basal triangular flat surface.

Length head and thorax 6.6 mm, abdomen approximately same length, fore wing 13.3 mm, rear wing 9.9 mm, genitalia length 1.25 mm, width 1.3 mm, subgenital plate length 1.8 mm, width 0.86 mm.

Type Locality.—Tela, Honduras. April. Bates (*MCZ*).

Priocnessus octomaculatus n. sp.

Figs. 3, 4.

Holotype male.—Body black, one-third of sides of clypeus, the anterior orbits broadly (from base of clypeus up to antennae) extending almost to top of eyes, each side of pronotum just before posterior border, a spot on middle of scutellum, posterior tip of propodeal side pieces (just above posterior coxae), a spot just in front of middle coxae, a spot each side on first tergite just before posterior edge, a spot in middle of first tergite, a very large spot on sides of second tergite, a large spot on sides of third tergite (almost touching in center), a large spot on sides of fourth tergite (almost hidden under telescoped tergite), the apex of all the femora, a narrow stripe on outside of fore tibiae, a broader stripe on outside edge of middle tibiae and the whole outside edge of posterior tibiae, whitish yellow. Mandibles whitish about center on inside edge; eyes reach vertex, the latter almost straight across but ocelli a little higher; temples very narrow, a small whitish spot just below vertex; clypeus very much raised, concave on front with a small tooth in center; numerous upright colored hairs on head, thorax, and propodeum; clypeus, thorax, coxae and legs with prostrate silvery pubescence; middle interocular 0.55 the transfacial distance; head as broad as long; lower and upper interocular distance equal; lateral ocelli two and one-half times as far from eyes as each other; antennae black, ratio of length of first four joints are as 15:6:17:20, very

slender; under side of antennae brown; top of head finely punctured; pronotum exceptionally short, hardly any dorsal surface, angulate on posterior edge; dorsal surface of thorex finely punctured, mesonotum more coarsely than the rest; postnotum about one-half as long as post-scutellum, cross ridged; propodeum short and whole length only slightly sloping; abdomen widest at apex of second tergite, there three times as wide as base of first tergite; upright hair on first tergite and a good deal on apex of last three tergites; wings almost hyaline but with a yellowish tinge in reflection; marginal cell long, one-half its length from wing tip, slightly wider than second cubital cell; third cell longer and broader than second cubital; second cubital cell about two-thirds as long on marginal vein as on cubitus, third about one-half as long; basal vein basad of transverse by the length of latter; in rear wings the subdiscoidal and cubital veins are interstitial; all spurs white, the longest spur of posterior legs about three-forths as long as basi-tarsus; very large arolia between claws.

Length head and thorax 5.3 mm, abdomen 5.3 mm, fore wings 9.9 mm, rear wings 7.0 mm, length genitalia 1.2 mm, width 1.0 mm, length subgenital plate 0.6 mm, width 0.46 mm.

Parts of genitalia all very short, aedeagus hardly 0.75 as long as volsellae, and the basal half hardly narrower than the apical half; parameres with a broad shallow concavity on inside basal half, rather sharp pointed; subgenital plate roof shaped, very broadly at base and tapering out at apex; widest above middle.

Type Locality.—Tepoztlan, Morelos, Mexico, August 20, 1956. R. R. and K. Dreisbach. (*USNM*).

Allotype female.—Markings as in the male; clypeus high, concave on apical edge with tooth in middle; interocular distance is 0.54 trans-facial, upper and lower interocular distances equal; head about 1.2 as wide as long; clypeus about 0.7 as long as wide; ratio first four antennal joints is as 12:4:18:14; third antennal joint about 0.9 the interocular distance at vertex; lateral ocelli about 1.75 as far from eyes as from each other; antennae long and slender; posterior orbits very narrow; about seven large teeth on posterior edge of hind tibiae; middle tibial joint with golden spines on posterior surface one-third to one-half width of joint; the teeth on posterior tibiae set near inner edge and a row of smaller teeth on outer edge, the space between bare and some-what concave; the large teeth set at an angle to the longitudinal length; the posterior edge of hind tibiae and the hair brush on inside yellow; the spurs white; spur of posterior tibiae one-half length of its metatarsal joint.

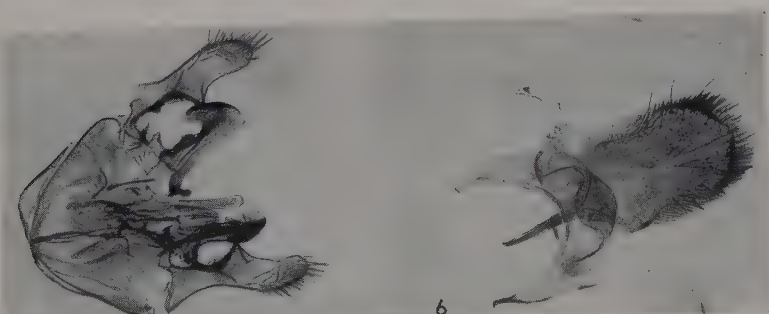
Length head and thorax 7.0 mm, abdomen 5.5 mm, fore wing 10.6 mm, rear wing 8.0 mm.

Other Localities.—Allotype female: Tepoztlan, Morelos, Mexico, August 20, 1956, R. R. and K. N. Dreisbach (*USNM*). Paratype females: two, Tepoztlan, Morelos, Mexico, September 26, 1957, R. R. and K. N. Dreisbach (*RRD*); two, Cuernavaca, Morelos, Mexico, September 29, 1957, R. R. and K. N. Dreisbach (*RRD, MCZ*); one, Carapu, Michoan, Mexico, September 2,

1938, L. J. Lipovsky (*USNM*); one, 8 miles NE. Taxco, Guerrero, Mexico, August 8, 1954, 5450 ft., Univ. Kansas, Mex. Exp. (*Univ. Kansas*).

Priocnessus orbiculatus (Smith)
Figs. 5, 6.

Body color black (particularly the thorax which is wholly black) with the thorax covered with a very beautiful fine silvery pubescence which in reflected light has a golden tinge; clypeus (except a linear black mark in middle, which extends to base of antennae), broad inner orbits which extends beyond fore ocellus, posterior orbits (broader in upper part), two preapical spots on sides of first tergite, posterior edge of first tergite, two broad spots on middle of sides of second tergite, same on third tergite and in addition a narrow band across posterior edge, a spot on middle of posterior edge of fourth tergite, apical bands across posterior edge of tergites five and six, and all of tergite seven, yellowish red; ventral surface of all coxae whitish; apex of trochanters, and all legs reddish yellow except last one or two tarsal joints of middle tarsi and all tarsal joints of posterior tarsi are blackish; antennae more or less blackish on dorsal surface and all of joint two black, underside reddish yellow except some black on last three or four joints; the first seven joints of antennae almost cylindrical, the eighth through tenth joints slightly hollowed out on under side, while the last three joints are increasingly flattened (hence the name) until the last joint is twice as wide as joints preceding the eleventh joint; clypeus strongly concave with a blunt tooth in the middle, strongly arched longitudinally, twice as broad as long; when seen from in front vertex straight across, the ocellar triangle slightly higher; the upper interocular distance 0.9 the lower interocular distance; the middle interocular distance 0.52 the transfacial distance; head approximately 1.2 as broad as long; lateral ocelli 1.5 as far from eyes as each other; ratio length first four antennal joints 12:3:18:16; very narrow posterior orbits; hardly any dorsal part to pronotum, transverse on posterior border; propodeum in sloping line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Figs. 5 and 6.—*Priocnessus orbiculatus* (Smith). 5.—Genitalia (x 30). 6.—Subgenital plate (x 30).

to apex, apex hardly lower than base, very heavily haired; whole thorax with numerous long upright hairs, fewer on abdomen; marginal long, one-half its length from apex of wing; basal vein in fore wing basad of the transverse by just about the length of the latter; in rear wing the subdiscoidal vein is just barely apicad of origin of cubitus; third cubital cell longer and broader than the second, extends nearer tip of wing than the marginal cell; inner claw of fore tarsi modified; the inner cleft part of the outer claw with broad base and the apical ray very close to it, the apical ray hardly curved on inside; the inner claw not so broad and considerable distance between the rays, the inner apical ray with deep curvature at base.

Length head and thorax 6.0 mm, length abdomen 6.0 mm, length fore wings 10.0 mm, length rear wings 7.2 mm, length genitalia 1.52 mm, width 1.06 mm, length subgenital 1.32 mm, width 0.53 mm.

The subgenital plate almost parallel-sided; the whole ventral surface of plate slightly raised above the sides; long haired around apex; the apical part of parameres apicad of the concavity on the inside longer than in other species (one-half the length of part).

Range.—El Salvador, Mexico.

Priocnessus flavidus n. sp.

Holotype female.—Black, whitish and yellowish; clypeus, face and front yellowish white, a black line from base of antennae to fore ocellus, the whole ocellar triangle and a line across vertex black; posterior orbits yellow with the back of head black; pronotum yellow except a black streak across the rise, posterior edge transverse; a large yellowish spot in middle of mesonotum over whole of scutellum except sides, a large yellowish spot under posterior wing and one each above middle and rear coxae, rest of thorax black; first tergite yellow with some black at base, second tergite with two large spots on side and posterior edge yellowish red; apical halves at least of tergites 3-6 reddish; first ventrite reddish, and posterior edge of rest of ventrite slightly reddish; coxae and trochanters whitish with some black; legs all reddish except tarsal joints are blackish; first two antennal joints and basal three-fourths of third joint yellowish, from there to apex black on dorsal surface brownish on ventral surface; clypeus with a blunt tooth in center of apex with sides concave each side of it; clypeus 2.25 times as wide as long, not very much arched on dorsal surface; lower interocular distance 1.2 times the upper interocular distance; interocular distance at middle 0.5 the transfacial distance; ratio lengths first four joints antennae are 14:5:24:20; the third antennal joint is almost 1.1 as long as width of vertex; head only very slightly broader than long; posterior orbits very narrow; lateral ocelli slightly more than 2.5 as far from eyes as each other; very short dorsal surface to the pronotum and not raised very high above neck; scutellum almost one third as long as mesonotum, raised, roof-shaped; propodeum in a very low slope; abdomen almost flat on dorsal surface and sides parallel from

middle of second tergites to almost tip of third; head and thorax, especially the propodeum with long abundant light hair; the light spots rendered silvery by reflection by the prostrate pubescence; posterior tibiae with a row of about 10 flat, rounded, thin, teeth, set crosswise of tibiae near inner edge, with a sharp longer tooth or spine set just behind them, the outer edge with a row of similar smaller teeth; claws with a sharp tooth near the middle; the space between the two rows of teeth and around them covered with long golden hairs; marginal cell 0.6 of its length from wing tip, the cell about same width as second cubital cell, rather narrow; third cubital cell very long almost twice as long as second and extends beyond marginal cell; first recurrent vein meets second cubital cell at apical third and second recurrent meets third cubital cell at basal third, both veins almost straight; the basal vein in fore wings apicad of transverse vein by 1.5 the length of latter (which is very short); in rear wings subdiscoidal vein is barely apicad (almost interstitial) of origin of cubitus.

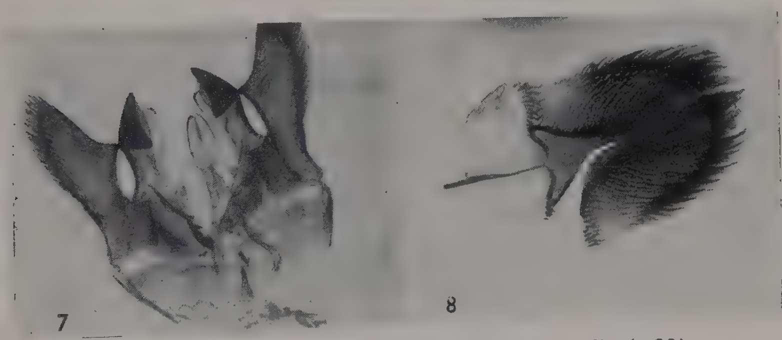
Length head and thorax 8.6 mm, length abdomen 6.7 mm, length fore wing 13.3 mm, length rear wing 9.3 mm.

Type Locality.—Rosario, Acatlan, El Salvador, July 22, 1955, 631 - 305 M.S.V. (*USNM*).

Priocnessus kayi n. sp.

Figs. 7, 8.

Holotype male.—Body black, head and thorax somewhat opaque, abdomen slightly shining; inner orbits to just above antennae, under side of third and fourth antennal joints, all of joints five through eight, under side of joints nine through twelve, tip of fore and middle femora inside of fore tibiae and posterior tarsal joints, light yellow; outside of fore tibiae, fore and middle tarsal joints, more or less blackish mixed with light reddish; face ventral parts of coxae and parts of thorax covered with brownish pubescence; head and thorax covered with fairly long dark hair; propodeum, first tergite, last two or three tergites



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Figs 7 and 8.—*Priocnessus kayi* n. sp. 7.—Genitalia (x 30). 8.—Subgenital plate (x 30).

and ventral part of abdomen with upright hair; clypeus with a large blunt tooth in middle of apex each side of which is deeply concave with two broad teeth each side; the sides of clypeus oblique, converging toward the front so that apical edge from the outside of the lateral teeth is only one-half width of basal edge, clypeus somewhat shining; the greatest width of clypeus is twice the length; the upper and lower interocular distance just about equal; middle interocular distance is equal to 0.51 transfacial distance; width of head equal to 1.1 the length; the lateral ocelli about twice as far from eyes as from each other; ocelli of equal size; ratio of first four joints of antennae are as 10:2:12:11; antennal joints 6 -8 have a lengthwise groove on inside and joints 9 -10 have a ridge on side; pronotum short, slightly angulate on posterior border; scutellum prominent, about twice as long as postscutellum which again is almost twice as long as metapostnotum, the latter slightly, transversely ridged; propodeum sloping from base to apex; wings rather reddish yellow with mottling or a slight dark band from marginal cell backward into the third discoidal; the apex of wings from tip of marginal cell to base of subdiscoidal vein blackish, the two dark areas giving a very prominent banded effect; tip of rear wing blackish, but not the rear edge; veins yellow but are darker in blackish areas; marginal cell long and narrow hardly wider than second cubital cell, about 0.6 its length from wing tip; third cubital cell wider and much longer than second, nearer margin of wing than the marginal cell, its length on marginal about equal to the length of second on the marginal; basal vein basad of transverse by just about the length of latter; first recurrent vein meets second cubital cell about the middle, the second recurrent meets the third cubital cell before the middle; in rear wings the subdiscoidal is slightly apicad of the origin of cubitus; posterior tibia has 8 or 9 good sized spines on dorsal edge (0.3 to 0.4 as wide as tibiae) surrounded by many hairs about 0.6 as long; claws cleft; the inner ray blunt and very short; longer spur of posterior tibia about one-half as long as metatarsal joint.

Length head and thorax 5.3 mm, abdomen 5.6 mm, fore wing 10.6 mm, rear wing 7.6 mm, length genitalia 1.06 mm, width 0.93 mm, subgenital plate length 1.20 mm, width 0.65 mm.

Subgenital plate with a basal triangular raised area which merges into a low ridge about center of plate and becomes almost evanescent at apex, the raised area bare of hair, rest of plate well haired with prostrate backward directed hair; very much like P. *dakota* but plate not nearly so heavily haired, nor hair as long nor as thick, nor does *dakota* have a row of heavier bristle across basal edge; genitalia similar to *dakota* but again parameres are heavily haired on surface whereas those of *dakota* are bare; the external characters of the adult are much different in the two species. This species is named for my wife Kay, who is an excellent collector. She has added many new species to our collection and even when we collect together she manages to get many species that I do not.

Type Locality.—Tepoztlan, Morelos, Mexico, August 20, 1956, R. R. and K. Dreisbach (*USNM*).

Priocnessus rubrus n. sp.

Holotype female.—Completely light red with the following black markings, dorsal surface of antennae beyond second joint, a streak under the head just behind the mandibles, a streak behind head just in front of neck, which continues and runs around base of fore coxae, the plate just under the tegula, a streak just at base of slope of pronotum, a narrow streak on posterior edge of mesonotum, the anterior margin and sides of scutellum, the metapostnotum and continuing on the suture past the spiracle to middle coxa continuing around rear coxa and across apex of propodeum (a line extending from apex of propodeum to the middle of propodeum which is very broad at apex of propodeum), the under side of thorax and the dorsal side of middle coxae, the base of posterior coxae underneath, and the base of the trochanters more or less; clypeus raised above mouth parts, arched sideways, and slightly concave on front; the clypeus when seen from underneath with just an indication of a tooth in the middle and slightly concave on each side; clypeus just about 2.0 as wide as long; lower interocular distance slightly longer than the upper (16:15); middle interocular distance 0.57 the transfacial; head slightly broader than long; posterior orbits medium, about one-half as wide as eyes; second and third antennal joints about equal to the upper interocular distance; ocelli same size, the laterals 2.5 as far from eyes as each other; ratio of first four antennal joints are as 18:4:24:20; pronotum short on dorsal surface; scutellum about one-third as long as mesonotum, both it and postscutellum raised slightly in middle, convex; metapostnotum about one-half as long as postscutellum, smooth; propodeum short on what might be considered dorsal surface, difference between plane of base and apex more than usual, in a very smooth curve; abdomen widest at apex of second tergite; head and thorax, including propodeum, well haired with fairly long light colored hair, but that on vertex and pronotum dark; abdomen with the last three segments well haired dorsally and ventrally; wings dark over whole surface, glistening in reflected light with a faint purplish sheen; marginal cell long and slender, not wider than the second cubital and 0.6 its distance to wing tip; third cubital cell 1.5 as long as second and 1.5 as long on marginal vein as the second; the third cubital cell extends about as far toward wing tip as marginal cell; a slightly darker cloud in first and second cubital cells, extending slightly into the third cubital and third discoidal cells; the veins of wings dark except the costa and subcostal veins and costal cell, as well as base of both wings are reddish yellow which is very noticeable; the two recurrent veins meet their respective cubital cells at the apical third and before the middle respectively; the basal vein basad of the transverse by the length of the latter; in the rear wing the subdiscoidal vein is apicad of the origin of

cubitus by about 3.5 the thickness of the vein; teeth with broad apex on inner dorsal edge of posterior tibiae, a slightly longer spine just behind each one; on outer edge an exactly similar row of teeth, the space between them slightly grooved and with short hair; these teeth set with the broad surface crosswise to length of tibiae; claws with a small tooth about middle and a pencil of bristles extending from base of claw to outer ray; a few spines under last joint of posterior tarsi.

Length head and thorax 9.3 mm, abdomen 10.0 mm, fore wing 14.7 mm, rear wing 10.6 mm.

Type Locality.—Tepoztlan, Morelos, Mexico, August 20, 1956, R. R. and K. Dreisbach (*USNM*).

Priocnessus aureus n. sp.

Holotype female.—Ground color black and red, with large conspicuous patches of golden and silvery pubescence; mandibles (except base), exposed mentum, apical third of clypeus, slope and dorsal part of pronotum, mesonotum (except side pieces) dorsal surface of scutellum, all dorsal part of abdomen (except basal 0.4 of first tergite), the posterior margins of the first five ventral segments, all of the sixth, and the first five antennal joints, a rather bright red; rest of body black with various patches of silvery and golden shining pubescence; golden, shining, prostrate pubescence on clypeus, face, front to the fore ocellus, posterior orbits, all the pronotum, part of mesonotum and part of scutellum; a large patch of more silvery pubescence on pleura just above middle coxa, at each outer posterior corner of propodeum, and across the base of propodeum; fore coxae and dorsal part of rear coxae also more or less silvery; long somewhat shaggy hair on clypeus, face, head, pronotum, fore coxae, and postscutellum; not so long or shaggy on propodeum, rest of coxae, sides of thorax and apical ventral segments; clypeus concave in front, no tooth and not raised above mouth parts in normal manner; clypeus 2.25 times as broad as long; eyes slightly convergent above, lower interocular distance is 1.15 times the upper; middle interocular distance 0.57 the transfacial distance; head slightly broader than long; lateral ocelli about 1.7 as far from eyes as each other; vertex not higher than eyes, ocelli hardly raised above vertex; ratio of first four antennal joints are as 16:5:29:22; second and third antennal joints just about as long as interocular distance at vertex; posterior orbits slightly more than one-half as wide as eyes; hardly any dorsal surface on pronotum, slightly angulate on posterior edge; mesonotum, almost flat in center, a slight ridge each side running forward from posterior side edge marking off a flange on fore edge as sides expand to pronotal shoulders; scutellum almost half as long as mesonotum, postscutellum more than half as long as scutellum and metapostnotum hardly visible on dorsal surface; propodeum short in a low curve to apex; abdomen widest at apex of second tergite; a very deep transverse groove near base of second ventral, the abdomen much expanded ventrally just beyond it; the fore wing with the fore part of

the whole wing deep brown the rear part (about half on the apical half) transparent as is all the rear wing; marginal cell long and narrow about as wide as second cubital cell; about 0.6 of its length from wing tip; third cubital cell exceptionally long about 1.6 as long as second, extends much beyond marginal cell, only about 0.4 its length from edge of wing, 2.5 as long on marginal cell as the second; the two recurrent veins meet cubital cells about apical fourth and in middle respectively; the basal vein apicad of the transverse in fore wings, less than the length of latter; the subdiscoidal vein in rear wings apicad of cubitus at least four times the width of vein; only one row of the flat, blunt, concave teeth on dorsal surface of posterior tibiae in middle of dorsal surface but divides into two rows about basal fifth; closer together but smaller than in preceding species *P. kayi;* claws toothed with a short tooth before middle and with long slender apical ray.

Length head and thorax 11.2 mm, abdomen 8.6 mm, fore wings 15.2 mm, rear wings 10.6 mm.

Type Locality.—Mexico, No. 2499, C. F. Baker (*USNM*).

Other Localities.—Paratype females: one, La Gloria Cardel, Vera Cruz, Mexico, 1938, J. Camelog, 4408 (*USNM*); one, 8 mi. NE. Taxco, Guerrero, Mex., August 8, 1954, 5150 ft. Univ. Kan. Mex. Exp. (*Univ. Kansas*); No label. Presumably from Mexico (*USNM*); one, Acayucan, Vera Cruz, Mexico, October 22, 1957, R. R. and K. N. Dreisbach (*RRD*).

The last paratype is smaller than the others, its measurements are: length of head and thorax 7.2 mm, abdomen 6.3 mm, fore wing 11.2 mm, rear wing 8.3 mm.

Priocnessus semirufus n. sp.

Holotype female.—Head black with white marks, thorax black with posterior edge of pronotum reddish, abdomen wholly, except base of first tergite and part of second and third ventral segments, black; sides of face, broad inner orbits to lateral ocelli, and a large spot on upper posterior orbits, white; posterior orbits not one-half as wide as eyes; first two antennal joints red, rest black; first three flagellar joints of medium thickness but antennae becoming increasingly slender to apex, the last joint is very slender; coxae black except tips are reddish, trochanters black and red, rest of legs reddish except last one or two tarsal joints are blackish; clypeus raised above mouth parts as usual, the front margin slightly extended in middle and slightly concave on each side; clypeus slightly arched, and sides oblique so that front margin only 0.66 as long as base; clypeus 2.0 as broad as long; middle interocular distance 0.57 of transfacial; lower interocular distance 1.3 upper interocular, eyes converging above; fore ocellus slightly larger, the lateral ocelli 2.7 as far from eyes as each other; ratio of first four joints of antennae 13:4:24:16; second and third joints antennae slightly longer than the upper interocular distance; hardly any dorsal part to pronotum, the posterior edge slightly angulate; scutellum almost one-half as long as mesonotum, postscutellum small not half as long as mesonotum, postscutellum small not half as long as the scutellum;

metapostnotum not much shorter than postscutellum, cross ridged; dorsal part of propodeum almost half length of propodeum, the dorsal part almost level, slope smooth but apex much lower than base, the clypeus, face, pronotum, sides of thorax, propodeum, ventral parts of thorax and under side of coxae with beautiful, golden prostrate, pubescence as well as numerous upright golden hair; long hairs on apex of most of ventral segments of abdomen; abdomen widest about apex of second tergite; dorsal edge of posterior tibiae with a row of teeth on each edge, the ones on inside edge largest; teeth are flat, thin, broad, almost parallel-sided of about eleven in a row, hardly half as long as thickness of tibiae and with a spine behind each one about twice as long; the rows well separated at base but almost come together and disappear before apex; longer spur of posterior tibiae about 0.4 as long as its metatarsal joint; claw with a sharp tooth and sharp apical ray; marginal cell long and narrow, 0.5 of its length from wing tip; third cubital cell very long, twice as long as second, twice as long on cubitus as on marginal; second cubital cell 0.75 as long on cubital vein as on marginal; basal vein much basad of transverse, about the length of latter; the two recurrent veins meet their respective cubital cells at apical third and middle.

Length head and thorax 10.0 mm, abdomen 11.3 mm, fore wing 16.6 mm, rear wings 12.6 mm.

Type Locality.—Huascary, Peru, Sept. 21, 1911, C. H. T. Townsend (*USNM*).

Priocnessus niger n. sp.

Holotype female.—Completely black with only mandibles slightly reddish; wings light yellow with slightly darker apex; clypeus, head, under head, and coxae long thick, almost shaggy haired; thorax, propodeum, apex of abdomen, part of first tergite, and ventral segment not quite so long or shaggy, black haired; clypeus only slightly concave in front, no tooth; rather strongly arched sideways; clypeus not quite twice as broad as long; lower interocular distance slightly more than upper; middle interocular distance 0.58 the transfacial; head slightly wider than long; ocelli the same size, the laterals 2.3 as far from eyes as each other; antennae black, slender and ratio of first four joints are 16:4:26:22; the third joint of antennae is equal to the upper interocular distance; posterior orbits very broad, as wide as eyes; pronotum very short; scutellum large, postscutellum of medium size, metapostnotum almost one-half as long as postscutellum and smooth, no cross wrinkles; propodeum with the dorsal surface slightly longer than usual; abdomen broadest at apex of second tergite, a good groove across second sternite; posterior tibiae with the usual flat teeth subparallel sided with broad blunt tips; the two rows with hardly any space between them, the spines back of the teeth twice as long, the surface of tibiae covered with hairs as long as teeth; marginal cell long and narrow, one-half its distance to wing tip; second cubital cell 1.4 as

long on cubitus as on marginal, receiving first recurrent vein at apical 5/8; third cubital cell 1.5 as long as the second; as long on marginal as the second, receiving second recurrent vein at basal 0.6, it extends well beyond the marginal cell; basal vein in fore wings basad of transverse, slightly more than the length of the latter; subdiscoidal vein in rear wing apicad of cubitus by about thickness of the vein; claws with a broad blunt tooth about middle and a fairly long sharp ray; longer spur of posterior tibia one-third length of metatarsal joint.

Length head and thorax 10.0 mm, abdomen 10.6 mm, length fore wing 14.5 mm, rear wing 11.2 mm.

Type Locality.—Mexico (*USNM*).

Other Localities.—Paratype females: Mexico City, Mexico, September 25, 1957, R. R. and K. N. Dreisbach, (*RRD*), Tepoztlan, Morelos, Mexico, September 26, 1957, R. R. and K. N. Dreisbach (*RRD*). The paratype from Tepoztlan has joints 4-7 of antennae yellowish.

Priocnessus sericeus n. sp.

Holotype female.—Head black with white markings, thorax black, abdomen red, except base of first tergite and ventral segment and a streak across groove on second sternite, which are black; mandibles, except tip and lower edge, sides of face, rather broad anterior orbits to lateral ocelli, and a small spot on posterior orbits just below temples, white; legs with tip of femora and rest of legs except apical tarsal joint (which is black), reddish; antennae with first two joints black, the third black with tip beneath and joints four and five and base of sixth beneath, white, rest of antennae black; ratio of first four joints antennae as 16:4:20:24; the side of clypeus on dorsal surface oblique from eye to apical margin, the side pieces at right angles to surface and this vertical surface concave; the concavity running from eyes around and across front making a slight preapical ridge on clypeus; clypeus slightly concave across apex from the corners; apical edge of clypeus only 0.66 as wide as base; clypeus twice as wide as long; surface of clypeus punctate, shining, slightly longitudinally ridged; lower interocular distance 1.3 times the upper; middle interocular distance 0.57 the transfacial distance; head 1.2 as broad as long; fore ocellus slightly the largest, the laterals 3.0 as far from eyes as from each other; second and third antennal joints equal to the vertex width; vertex at level of eyes, ocellar triangle slightly raised; posterior orbits about 0.5 as wide as eyes; temples very narrow; pronotum very short; mesonotum finely punctate, a slight ridge extending forward from just behind tegula parallel to axis of body forming an angle with the raised side border; scutellum finely punctate; postscutellum about 0.5 as long as scutellum, transversely ridged; metapostnotum about 0.3 as long as postscutellum, and slightly cross-ridged; propodeum with a very short dorsal surface before the smooth slope; abdomen broadest about the apical 0.25 of second tergite; wings almost hyaline but slightly brownish; venation

about as usual; recurrent veins meeting their respective cubital cells at apical 0.33 and basal 0.33; basal vein basad of transverse about length of latter; in rear wings subdiscoidal vein apicad of cubitus by 2.0 thickness of a vein; posterior tibiae as usual with the two rows of teeth with hair between; claws as usual; clypeus, face and all thorax with beautiful, appressed, glistening, silvery pubescence (hence the name); long light colored hairs over, head, thorax, coxae, first tergite, first sternite, last tergite, and more or less over whole sternite.

Length head and thorax 8.6 mm, abdomen 10.0 mm, fore wing 15.2 mm, rear wing 11.2 mm.

Type Locality.—Bogota Colombia, 1931. B. Guevara. (*USNM*).

Other Locality.—Paratype female: Colon, C. F. Baker (*USNM*).

Priocnessus opacus n. sp.

Holotype female.—Body completely black, no marks or color except on antennae; first two joints, basal three-fourths of third and joints 8-12 black, apical quarter of third and 4-7 lemon yellow; the whole thorax opaque, head and abdomen slightly shining; fairly long, thinly placed, hair under head, on coxae and a few on ventral segments; shorter hair on upper part of head, thorax, propodeum, the preceding all blackish, but fairly long dense prostrate ochreous hairs on last tergite; a broad flange in center of front margin of clypeus, the front concave on each side to broad short flanges on the side; clypeus 2.0 broad as wide; lower interocular distance 1.2 the upper; middle interocular distance 0.5 the transfacial; third antennal joint equal to the vertex width; ratio of first four antennal joints is as 14:4:20:14; head 1.2 as broad as long; vertex straight across; hardly any posterior orbits and temples evanescent; occipital carina extends to pregular suture; pronotum very short, postscutellum 0.3 length scutellum and metapostnotum about 0.5 the length of postscutellum, with a few cross ridges; propodeum in a smooth curve to apex; spines on tibiae and tarsi golden, and the tips of tarsal joints are inclined to be reddish; posterior tibiae with exceptionally large teeth on inside edge of dorsal surface, the outer row very close to them and very few hairs between, surface shining; claws as usual, a few spines on under side of last joint; wings yellow with a much darker apex in fore wings, the dark covering the outer half beyond cells, and extending on rear edge to base of third discoidal cell; rear wings with narrower band and not quite so strong but extends around rear of wings to base; third cubital cell extends beyond marginal cell; first recurrent vein meets second cubital cell in *middle,* the second recurrent meets third cubital about basal 0.4; basal vein in fore wing apicad of transverse slightly more than length of the latter; in rear wings subdiscoidal vein is apicad of cubitus by width of vein.

Length of head and thorax 6.7 mm, abdomen 8.0 mm, fore wings 11.9 mm, rear wings 7.6 mm.

Type Locality.—Tepoztlan, Morelos, Mexico, August 20, 1956, R. R. and K. N. Dreisbach (*USNM*).

Priocnessus tricoloratus n. sp.

Holotype female.—Color black, red, and white; head black with base of mandible (0.75 of length), clypeus (except apical edge and black streak in middle), two large spots on anterior orbits between antennae and fore ocellus, spot on posterior orbits just above mandibles, and a spot on upper posterior orbits, white; thorax black with a spot at each outer corner of neck, posterior border of pronotum (except spot in middle) and extending on sides to include tubercle, a large spot in middle of posterior part of mesonotum, a band across scutellum, band across postscutellum, a large elongate spot on mesopleura above middle coxae, an elongate spot under each posterior wing, and a large spot on outer posterior corners of propodeum extending inward along rim, white; abdomen red except base of first tergite, ventral surface and sides of fore coxae, white; fore femora and tibiae black with white streaks; middle coxae reddish and white; middle and posterior femora red; posterior pair of legs all red but last tarsal joint is blackish; middle tibiae and tarsi blackish with some reddish yellow spines; clypeus raised, front almost truncate with a rim; front, vertex and dorsum of thorax finely, smoothly, punctured; fairly long light colored hairs on clypeus, face, under head, coxae, sides of thorax, and propodeum; the fairly long hairs on head and vertex black; long hairs on last tergite reddish; clypeus 2.25 as broad as long; lower interocular distance equal to 1.15 the upper; middle interocular distance 0.5 transfacial; fore ocellus the largest, the laterals 2.0 as far from eyes as each other; head 1.45 as broad as long; anterior orbits very narrow, temples only a line; very short metapostnotum; propodeum in a smooth curve; abdomen broadest about middle of third tergite; posterior tibiae with inner row of teeth on dorsal surface very small, hardly rising above surface but spines of about usual size; outer row with no teeth but spines of same size as other row; only one row at base of tibiae which then divides into the two rows; antennae black except apical half of sixth, seventh, eighth and basal half of ninth are white; ratio of lengths of first four joints are 15:5:20:19; wings hyaline, with faint blackish tip; basal vein basad of transverse by length of latter, which is short; first recurrent meets cell in apical third and the second before the middle; in rear wing subdiscoidal vein is almost interstitial with cubitus.

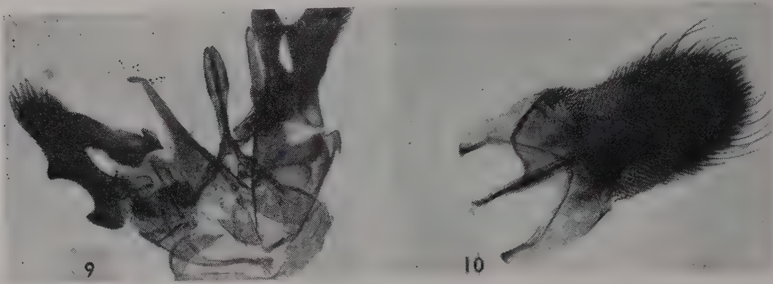
Length of head and thorax 7.3 mm, abdomen 7.9 mm, fore wing 13.5 mm, rear wing 11.2 mm.

Type Locality.—Rio de Janeiro, Brazil, September, 1938, Yel. Fev. Survey M E G. R. C. Shannon (*USNM*).

Other Locality.—Paratype female: Nova Teutonia, Santa Catarina, Brazil, December 21, 1952, Fritz Plaumann (*RRD*).

Priocnessus lineatus n. sp.
Figs. 9, 10.

Holotype male.—Completely black except for a white line on anterior orbits on face; antennae wholly black; antenna has a ridge on



Figs. 9 and 10.—*Priocnessus lineatus* n. sp. 9.—Genitalia (x 30). 10.—Subgenital plate (x 30).

underside (lengthwise) which bears a row of short curved hair, hardly evident on first four and last joints; the head, fore coxae, neck, pronotum, and propodeum with very long, dense, black hair; rest of thorax, last two pair of coxae, first tergite, last three or four tergites, and ventral surface with much shorter black hair; clypeus very much raised above mouth parts and strongly arched; clypeus with three broad teeth, the apical edge concave each side of middle tooth; clypeus 1.6 times as wide as long, the sides oblique from eyes to apical edge, the apical edge 0.6 as wide as base of clypeus, the apical edge as wide as lower interocular distance; the upper interocular distance 1.1 as wide as the lower; the middle interocular distance just about 0.5 the transfacial; head slightly longer than broad, approximately 1.1; ratio of first four joints of antennae as 22:4:16:16; posterior orbits about 0.5 as wide as eyes, temples well evident; ocelli of equal size, laterals 2.0 as far from eyes as from each other; very short pronotum, angulate on posterior border; the sides of mesonotum slightly raised and a line from just behind tegula extending forward parallel to axis of body about half way to anterior edge; scutellum and postscutellum raised on dorsal surface, metapostnotum very evident, smooth and 0.5 as long as postscutellum; propodeum in a very low slope; abdomen widest at apex of third tergite; posterior tibiae with two rows of small teeth and spines, an exact replica of the posterior tibiae of female, but spines and teeth smaller, and two rows closer together; longer spur of posterior tibiae not quite 0.3 length of its metatarsal joint; claws cleft; fore tibiae almost free of spines, middle tibiae well spined; subgenital plate visible as a broad flat basal, hairless plate which narrows about middle of plate, long haired at the sides of this raised area of plate; wings reddish with black tip, extending over outer edge, the rear wings with the tip not so dark but the dark color extends over whole rear of wing; first recurrent vein meets second cubital cell at *middle,* the second meets third cell a little before middle; basal vein basad of transverse by the length of latter; subdiscoidal vein in rear wing apicad of cubitus by width of vein.

Length head and thorax 6.6 mm, abdomen 6.6 mm, fore wings

11.6 mm, rear wings 8.8 mm, length genitalia 1.7 mm, width 1.3 mm, length subgenital plate 1.7 mm, width 0.8 mm.

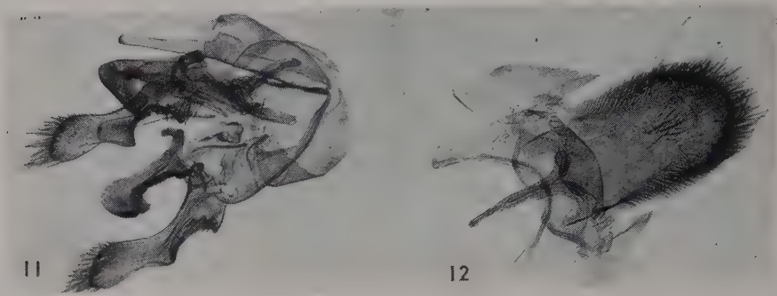
Type Locality.—Rio Blanca, Vera Cruz, Mexico, November 13, 1957, R. R. and K. Dreisbach (*USNM*).

Other Localities.—Paratype males: one, same data as type (*RRD*); five, Tepoztlan, Morelos, Mexico, September 26, 1957, R. R. and K. N. Dreisbach (*RRD*); two, Cuernavaca, Morelos, Mexico, September 28, 1957, R. R. and K. N. Dreisbach (*RRD; MCZ*).

One paratype from Tepoztlan has the apex of fourth antennal joint and the next three antennal joints yellowish, but in every other respect is the same as the rest.

Priocnessus ornamentatus n. sp.

Holotype female.—Body black, much ornamented with yellowish and reddish; front, vertex, head behind, thorax (with large spots more or less all over) and coxae more or less, with beautiful, golden pubescence; long, golden hair on mouth parts, under head, on fore coxae, propodeum, on ventral surface of abdomen, and last tergite; shorter light hair on most of rest of body; mandibles, all but apex, a large spot each side at base of clypeus, broad inner orbits to anterior ocellus, and upper posterior orbits, light yellowish; no marks on thorax; a broad preapical band on first tergite, two broad triangular spots on posterior preapical corners of second tergite, successively smaller spots in similar locations on tergites 3-6, yellow; the posterior edge of first four tergites reddish, and almost all dorsal surface of last two; first four sternites black, mottled with reddish, and last two completely reddish; coxae and trochanters black with apex reddish, rest of legs reddish except last two to four joints of tarsi, blackish with reddish spines; antennae all black with apex of first joint reddish; clypeus arched and raised above mouth parts, a broad very short tooth in center of apical edge, with edge each side of tooth concave on front edge; front edge of clypeus 0.6 as broad as base, the breadth of clypeus slightly more than twice the length; lower interocular distance 1.2 the upper; middle interocular distance 0.5 the transfacial; head 1.15 as broad as long; fore ocellus slightly the largest, the laterals about 2.3 as far from eyes as each other; ratio of first four joints of antennae is 12:4:20:16; the third antennal joint equal to the vertex width; posterior orbits about 0.67 as wide as eyes; hardly any temples; vertex straight across from eyes, ocellar triangle slightly higher; pronotum very short; mesonotum short, twice as long as scutellum, postscutellum one-half as long as scutellum, metapostnotum almost 0.6 as long as postscutellum, with a few cross ridges; propodeal slope in a smooth curve; posterior tibiae as usual except very short distance between the two rows of teeth and those on outer edge are very short and narrow; longer spur of posterior tibia 0.4 length of the basitarsus; claws as usual; first recurrent vein meets second cubital cell at apical third and the second recurrent meets third cubital at basal third; the basal vein is basad of transverse vein,



Figs. 11 and 12.—*Priocnessus prominens* Banks. 11.—Genitalia (x 15). 12.—Subgenital plate (x 15).

1.5 the length of transverse vein; in rear wings the subdiscoidal is interstitial with the cubitus; wings yellowish hyaline, veins yellow.

Length head and thorax 7.3 mm, abdomen 6.4 mm, fore wings 10.6 mm, rear wings 8.6 mm.

Type Locality.—Cerro Verde, El Salvador, September 11, 1956, 714-29, P.A.B. (*USNM*).

Priocnessus prominens Banks
Figs. 11, 12.

Male.—Head black, with base and upper edge of mandibles, mentum, clypeus (except a small basal spot) face (except a continuation of black of clypeus) broad inner orbits to lateral ocelli, a spot on upper posterior orbits, whitish; thorax black with neck whitish and tegula reddish; thorax covered all over with brilliant patches of beautiful prostrate golden pubescence; abdomen deep red except base of first tergite (both ventrally and dorsally) is black, and apical half of ventral part is blackish; first two joints of antennae completely red, rest of antennae black on top, brown underneath; joints of antennae long and slender, slightly hollowed in center; coxae blackish more or less on base and dorsal surface, reddish on ventral surface; rest of legs red except last one or two tarsal joints are black; a very strong rather sharp tooth on apex of under side of last trochanter; under side of head, fore coxae and propodeum with long, golden hair, the rest of head and thorax, first tergite and apex of abdomen with considerable, much shorter, hair; clypeus very much arched, and raised above mouth parts, deeply concave on apex with a small broad tooth in middle; clypeus 2.5 as broad as long, front edge 0.6 as wide as base; lower interocular distance 1.25 as long as upper; the middle interocular distance 0.56 as long as transfacial; fore ocellus the largest, the laterals 2.0 as far from eyes as each other; ratio of length of first four antennal joints is as 12:5:20:19; the second and third joints about as long as vertex width; metapostnotum about 0.3 as long as postscutellum; wings yellowish hyaline; both recurrent veins meet their respective cells at basal third; the basal

vein in fore wings basad of transverse vein by more than length of latter; in rear wings subdiscoidal vein is interstitial with the cubitus; posterior tibiae has small teeth and spines three times as long with long hair between.

Before dissection the subgenital plate shows a hairless raised surface triangular in shape at base as broad as visible part and extending the length of plate, triangle not closed at apex; plate rectangular and with spines around sides and apex, those on apical half and around the broad, blunt apex the longest; genitalia characteristic; the parameres with apical half broad and blunt, the basal half with a very deep concavity on inside.

Length head and thorax 7.4 mm, abdomen 6.0 mm, fore wing 12.0 mm, rear wing 10.0 mm, length genitalia 1.4 mm, width, 0.53 mm, subgenital length 1.59 mm, width 0.66 mm.

Range.—Peru, Colombia.

Priocnessus caesius n. sp.

Holotype female.—Head and thorax with ground color bluish-gray (hence name), abdomen completely red; two spots on basal outside corners of clypeus, interior orbits to fore ocellus, a spot on temples back of eyes, reddish; pronotum appearing a deep red, the posterior margin transverse; the head and thorax covered with a fine pubescence, very strongly silvery on sides of propodeum; propodeum very short; coxae and trochanters black, suffused with reddish, rest of legs red; clypeus well arched and above mouth parts, a rim on front edge; front edge slightly concave; basal width of clypeus 1.60 width of apex, 1.9 as broad as long; lower interocular distance about 1.3 the upper; middle interocular distance is approximately 0.5 the transfacial; fore ocellus much the largest, the laterals 2.0 as far from eyes as each other; apex of third joint and forth and fifth joints bright yellow, rest black; ratio of first four joints of antennae is 15:4:24:20; the third joint of antennae slightly longer than vertex width; wings light yellowish, subhyaline; first recurrent meets second cubital cell beyond apical third and the second meets third cubital about basal third; in fore wings basal vein basad of transverse the length of the latter; in rear wings the subdiscoidal apicad of cubitus the width of a vein.

Length head and thorax 7.9 mm, abdomen 6.5 mm, fore wing 13.2 mm, rear wing 10.2 mm.

Type Locality.—Ecuador, C. F. Baker (*USNM*).

Priocnessus anomalus n. sp.

Holotype female.—Head and thorax black, with yellowish and reddish markings, abdomen rufous with yellow markings; mandibles (except base), clypeus, visible part of mentum, inner orbits to above antennae, and a small streak in upper posterior orbits, reddish yellow; posterior edge of pronotum and lower edge, a small spot in

middle of posterior part of mesonotum, most of scutellum, center of postscutellum, and a small streak across dorsal part of propodeum, reddish and yellow; abdomen with base of first tergite black and yellow, and a spot on sides of second tergite yellow; ventral part of abdomen black suffused with reddish; antennae with the first six joints red, the last six black; clypeus hardly raised above mouth parts, the front margin slightly wavy and only slightly projecting under eye; vertex slightly arched above eyes, the ocellar triangle slightly higher; upper and lower interocular distance the same; middle interocular distance is 0.5 the interfacial; fore ocellus slightly larger and laterals 2.0 as far from eyes as from each other; clypeus slightly more than 2.0 times as broad as long; head about as broad as long; ratio of first four antennal joints is as 14:4:30:25; third antennal joint slightly longer than vertex width; pronotum short, very slightly angulate behind; scutellum and postscutellum both raised in center, slightly cone-shaped; metapostnotum very broad, 0.7 as long as postscutellum, slightly wrinkled; propodeum very low; posterior tibiae with the teeth on inner edge very broad at base and becoming smaller and almost fading out before apex, the teeth concave in front and yellow with the inner edge reddish; coxae, trochanters and base of femora to one-half of femora, and rest of legs reddish, including all of tarsal joints; wings slightly like those of *aureus*, the fore half of fore wings deeper yellowish than the rear half and the rear wings; the basal vein basad of transverse by *less* than the length of the latter; in rear wing the subdiscoidal vein apicad of the cubitus by 4 or 5 times the width of vein; first recurrent vein meets second cubital cell at apical third and second recurrent meets third cubital at basal fourth; head, postscutellum, and propodeum fairly well haired with golden hair, rest of body with much shorter and much less hair.

Length head and thorax 8.6 mm, abdomen 9.9 mm, fore wing 15.6 mm, rear wing 11.1 mm.

Type Locality.—Guadalajara, Mexico, September 17, 1957, R. R. and K. N. Dreisbach (*USNM*).

This species has several characteristics slightly different than most species of the genus. The clypeus is hardly raised above mouth, the eyes are rather strongly emarginate just above base of antennae, the sides of clypeus hardly extend under eyes, the scutellum and postscutellum are much raised above surface of mesonotum (especially the postscutellum is almost cone-shaped), the teeth on inner edge of dorsal surface of posterior tibiae are very strong (and strongly concave on front) at base and become successively shorter and fade out before apex, the basal vein in fore wings is basad of transverse vein by a smaller distance than the length of the transverse, in rear wings the subdiscoidal vein is a greater distance apicad of the cubitus than is usual (about 5 times the width of a vein) in the species from Mexico and southward; the U. S. species have this vein apicad of cubitus a greater distance.

Priocnessus hurdi n. sp.

Holotype female.—Completely rufous except for the following black markings: apical third of mandibles, the dorsal part of thorax just back of attachment of fore wings back to and including a streak across base of propodeum, the latter extending downward on sides to the suture, the side of thorax below pronotum and the whole ventral surface of thorax including ventral surface of coxae and the transverse groove on second ventral segment; the first two and base of third antennal joints red above and below; the rest of antennae below reddish, the dorsal surface black; wings trifasciate with a black band across basal veins from subcosta to rear of wing, a second black band from basal third of marginal cell back to rear edge of wing, expanding in width to rear where it continues backward along rear edge to meet the black band across apex; wings yellowish, not clear, the veins reddish yellow except in dark areas, the stigma also reddish yellow; rather long, scant black hair on front, vertex and on dorsum of scutellum and postscutellum, hair on rest of body yellow; front margin of clypeus produced at corners, and less in the middle with edge slightly concave each side of center; clypeus 2.0 as broad as long; eyes slightly converging above, upper interocular distance is 26, lower 30 (on same scale as antennal measurements) ratio of lengths of third and fourth antennal joints is 20:18; head about 1.1 as broad as long; ocelli 2.0 as far from eyes as each other; the teeth on inner edge of posterior tibiae (the larger row of teeth) with the outer edge (about 0.3 of width) darker, this dark stripe extending across apex and a short distance on inner edge.

Length head and thorax 7.3 mm, abdomen 8.0 mm, fore wing 13.2 mm, rear wing 9.20 mm.

Type Locality.—10 km. W. of Zetacuaro, Michoacan, Mexico, July 11, 1951. P. D. Hurd (*USNM*).

Other Localities.—Paratypes (8): two, same data as type (*Hurd; MCZ*); two, Alpuyeca, Morelos, Mexico, July 3, 1951, Hurd (*Hurd; RRD*); one, Alpuyeca, Morelos, Mexico, June 27, 1951, Hurd (*Hurd*); one, 15 km. E. Sombrereta, Zac., Mexico, July 28-31, 1951, Hurd (*RRD*); one, Ahuacatlan, Nyarit, Mexico, July 18, 1951, Hurd (*Hurd*); one, 16 mi. S. of Cuernavaca, Morelos, Mexico, Aug. 22, 1958, H. Howden (*Howden*).

A few of the paratypes have more black on the dorsum of thorax, the color of antennae also varies. In some specimens the first one or two joints of antennae are red, above and below, the third, fourth and basal half of fifth are black, the apical half of fifth, the sixth and basal half of seventh white, the rest of antennae black. The bands on wings also vary, some not so black or covering less area. Otherwise they are uniform.

The paratype from Ahuacatlan was pinned on the same pin with an immature female spider of the genus *Euagrus* determined by Gertsch. This record was discussed in the literature by P. D. Hurd, Jr. and Marius S. Wasbauer (1956, *Jour. Kan. Ent. Soc.*, 29(4):169).

Priocnessus durangoensis n. sp.

Holotype female.—Head all black except a preapical reddish mark on mandibles, and a yellowish short, narrow, mark on interior orbits from antennae to fore ocellus; thorax, coxae and trochanters completely black; abdomen completely rufous except black at extreme base; basal 0.75 of fore femora black, and base of last two pair femora black, rest of legs completely rufous; apex of third joint of antennae, the fourth, fifth, and basal third of sixth joint white, rest of antennae black; clypeus slightly produced on outer front edges, the middle also slightly produced, thus with a slight concavity each side of middle; a narrow, shining, hairless rim on front edge of clypeus; clypeus 3.0 as broad as long; upper interocular distance (23) slightly less than the lower (26); ratio of lengths of third and fourth antennal joints is 22:18; head 1.2 as broad as long; lateral ocelli 2.5 as far from eyes as each other; silvery pubescence on head and thorax; considerable long white hair under head, dorsal surface of head and propodeum; wings hyaline, slightly dusky (yellowish), veins and stigma yellowish; basal vein in fore wing basad of the transverse by 1.5 the length of transverse; in the rear wings the subdiscoidal vein is apicad of cubital vein by just about the width of a vein; fore femora with a few long hairs on under side.

Length of head and thorax 6.6 mm, abdomen 7.8 mm, fore wings 11.5 mm, rear wings 9.6 mm.

Type Locality.—El Salto, Durango, Mexico, Aug. 3, 1951, P. D. Hurd (*USNM*).

KEYS TO SPECIES OF NEOTROPICAL PRIOCNESSUS

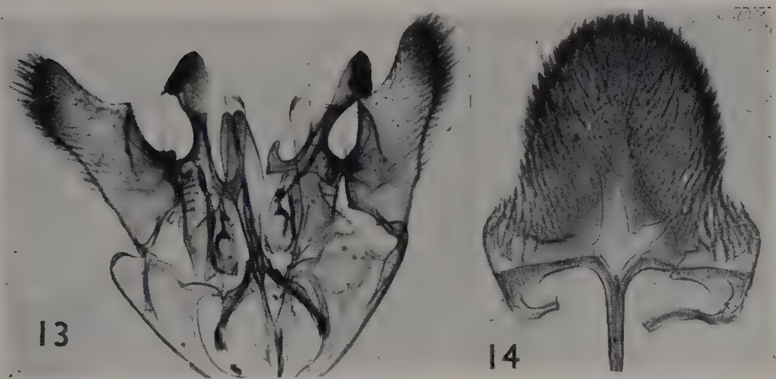
KEY TO MALES

1. Clypeus yellow, with a large black spot in middle, anterior orbits broadly yellow; mandibles largely yellow, tip and generally lower edge black; abdomen black, marked with rufous or yellowish or wholly rufous; wings hyaline or slightly yellowish, wings not banded, tips of wings *not* black; antennae black or black on dorsal surface, dark brown on under side, or in one case black with third and fourth joints yellow 2

1. Clypeus with no yellow marks whatever; in one case very narrow anterior orbits yellow; mandibles all black; abdomen black; wings strongly yellowish with black tip and in one case slightly banded; antennae black or some of middle joints yellow 5

2. Last trochanter with a strong tooth on apex of under side *and* abdomen red, legs red (including under side of coxae) except last two or three tarsal joints which are black; first two joints of antennae red, the rest black; head and thorax with golden prostrate pubescence spotted over most of surface; wings rather strongly fumous, yellowish; subgenital plate somewhat elevated, rectangular, with spines over apical sides and across apex. Peru and Colombia, (Figs. 11, 12) ....*prominens* Banks

2. Last trochanter with no tooth or with only an indication of one; abdomen black with yellowish spots or fuscous with yellowish spots; basal two joints of antennae black, rest of antennae black or brown on underside; head and thorax adorned with golden, silvery or no pile; wings almost



Figs. 13 and 14.—*Priocnessus apache* (Banks). 13—Genitalia (x 45). 14.—Subgenital plate (x 45).

hyaline with yellow veins or flavo-hyaline with testaceous veins; subgenital plate either similar to preceding or not rectangular but with sides concave near center 3

3. Wings with cloud over basal and transverse veins, from base of marginal cell backward over second cubital cell, and over apical half of third discoidal cell, and apex of wing beyond cells black; wings dark yellowish, costal vein *yellow,* rest of veins dark; clypeus, posterior orbits, all of pronotum, mesonotum, scutellum, and abdomen, red; legs also red. U.S. and Mexico. (Figs 13, 14.) .... *apache* (Banks)

3. No cloud whatever in wings; costal vein *not yellow* with rest of veins dark; body without the parts listed above all red 4

4. Pubescence of head and thorax without the least tinge of golden only slightly silvery *and* a few very small maculations on thorax; two narrow preapical lines on pronotum, large spot on scutellum, a faint mark each side just above middle and posterior coxae, yellow; abdomen black with a mark on middle of dorsal surface of first tergite, one on each side just before apex on first tergite, a large spot each side on second, third, and fourth tergites, yellow; legs *black* with the knees of femora and a stripe on posterior edge of tarsi yellow; antennae brown beneath, black above; wings hyaline; no tooth on posterior trochanter. Mexico. (Figs. 3, 4.) .... *octomaculatus* n. sp.

4. Pubescence of the head and thorax golden or strongly silvery with a trace of golden; no maculations whatever on thorax; abdomen blackish with maculations more numerous and reddish or fuscous with yellow marks; legs ferruginous; there may be an indication of a small tooth on posterior trochanter; antennae reddish on under side, dorsal surface blackish, *and* the last three joints much enlarged and flattened, whitish mottled with black; first tergite with yellow and reddish markings just before apex, two reddish spots on sides of second and third tergites, the posterior border of all tergites 2-6 reddish, the seventh tergite wholly reddish; subgenital plate rectangular with a raised hairless area over most of surface. Costa Rica. (Figs. 5, 6.) .... *orbiculatus* (Smith)

5. Narrow yellow lines on anterior orbits from base of clypeus or just above; clypeus with three teeth on front margin, middle one small triangular,

the sides concave each to the lateral broader teeth; clypeus much raised above mouth parts, strongly arched 6

5. No marking on anterior orbits, body wholly black; clypeus *without* teeth concave on front margin or almost truncate 8

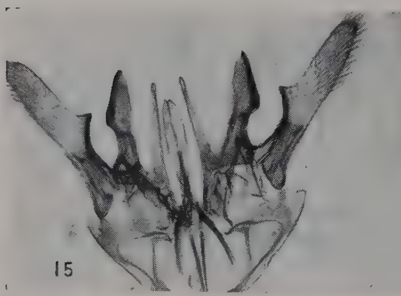
6. Antennae wholly black; wings reddish with contrasting black tip; subgenital plate elongate, gradually narrowing from base to broad obtuse apex; a few long hairs almost as long as width of plate on sides near apex and around apex; a raised hairless area, broad at base then gradually converging to apical fourth, sides above base subparallel; parameres of genitalia with a large concavity on outside near base. Mexico. (Figs. 9, 10.) ....*lineatus* n. sp.

6. Antennae with some joints completely yellow; wings reddish with a black cloud in second cubital and third discoidal cells, or hyaline with black veins; subgenital plate shorter and ovate, or as long but sides concave just above base 7

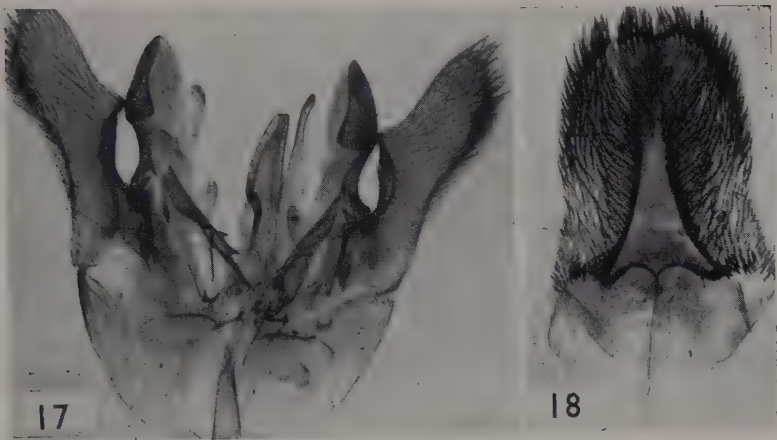
7. Antennal joints 5-8 completely yellow, joints 3, 4 and 9-11 yellow beneath, black on dorsal surface; linear impressions on joints 6-8; wings reddish yellow with a blackish cloud in second cubital and third discoidal cell; apex of wing blacker than in *lineatus* covering most of surface beyond the cells and extending around rear of wing to base of third discoidal cell; subgenital plate much shorter than in *lineatus,* ovate, triangular area shorter, not as broad; shorter hair on sides and around apex; parameres of genitalia short and broad, the outside edge straight without a large concavity. Mexico. (Figs. 7, 8.) ....*kayi* n. sp.

7. Some of middle antennal joints yellow; wings hyaline with dark veins; subgenital elongate, with the sides just above base concave, a broad basal triangle which is open at apex, the prominent sides of triangle ending about middle of plate; parameres of genitalia much more slender and longer than in *kayi.* Panama. (Figs. 15, 16.) ....*neotropicalis* (Cameron)

8. Head and thorax with hair black, only slightly reddish in reflected light, no appressed reddish pubescence; clypeus hardly raised above mouth parts and truncate in front; eyes reach vertex; pronotum transverse behind; subdiscoidal vein of rear wing is interstitial with the cubitus; no teeth and only a very few small spines on posterior tibiae; subgenital plate concave on sides about middle, the upper half of plate semiorbicular, the raised portion at base wider than in next; smaller size about 13 mm long. Honduras. (Figs. 1, 2.) ....*hondurensis* n. sp.



Figs. 15 and 16.—*Priocnessus neotropicalis* (Cameron). 15.—Genitalia (x 30). 16.—Subgenital plate (x 30).



Figs. 17 and 18.—*Priocnessus rogersi* Dreisbach. 17.—Genitalia (x 30). 18.—Subgenital plate (x 30).

8. Head and thorax with reddish black hair and with appressed reddish pubescence; clypeus raised above mouth parts and concave on front margin; pronotum angulate behind; subdiscoidal vein in rear wings apicad of cubitus; small teeth and spines on dorsal surface of posterior tibiae; subgenital plate almost rectangular, only slightly concave on sides near middle, the upper half with sides parallel to close to apex; size larger, about 15 mm. Mexico. (Figs. 17, 18.) ....*rogersi* Dreisbach

KEY TO FEMALES

1. White or yellow maculations on the thorax (*not* glittering spots of pubescence), head also well maculated, abdomen black with a great deal of yellow or completely rufous; wings white hyaline or slightly to strongly yellowish hyaline 2
1. No maculations on thorax but patches of silvery or golden pubescence may seem like maculations; wings generally strongly fuscous yellowish or reddish, in only about two species are wings yellowish hyaline 4
2. Clypeus with a small broad tooth on middle margin, margin each side concave; abdomen black, most of dorsal surface of first tergite yellow, two very large spots on sides of second tergite and two smaller ones on sides of third tergite, reddish yellow; first three joints antennae reddish, the rest black above, brown beneath; mandibles (except black apex), all clypeus, all face, front and broad anterior orbits to vertex, yellowish white, except a black streak in middle of front; posterior orbits all yellowish white; most of pronotum, a broad spot on mesonotum, band across scutellum middle and posterior edge of postscutellum, a large spot above middle coxae, smaller one under rear wing, the outer posterior corners of propodeum, and a spot above rear coxae, yellowish white. Costa Rica ....*flavidus* n. sp.
2. Clypeus almost truncate in front; abdomen almost completely rufous on dorsal surface, base of first tergite is black and may have a yellow

spot on base of first and sides of second tergite; rather broad anterior orbits, a spot on upper posterior orbits, a spot on posterior middle of *mesonotum,* dorsal surface of scutellum, and postscutellum, yellow or yellow with some reddish 3

3. Antennae with first five and one-half joints and last three and one-half joints black, joints in between yellow; mandibles except apex, clypeus except black spot in middle), posterior edge of pronotum (except in middle) extending downward and covering tubercle, a large spot just above middle coxae, a large spot under rear wing, a large spot on outer posterior corners of propodeum continuing on outer corner of rim, and ventral surface of fore and middle coxae, white; fore tibiae black and white, posterior femora and tibiae red; fore tarsi, middle tibiae and tarsi and last joint of posterior femora and tibiae, red; fore tarsi, middle tibiae and tarsi and last joint of posterior tarsi black; ventral surface of abdomen reddish suffused with black; wings almost hyaline. Brazil ....*tricoloratus* n. sp.

3. Antennae with first seven joints reddish (dorsal surface blackish), the rest black; mandibles (except base and apex), all of clypeus, lower side edge of pronotum, and legs beyond femora, reddish; broad posterior border of pronotum yellow with a reddish front edge; coxae, trochanters, and about basal half of femora black; abdomen with base of first tergite black and yellow and a yellow spot each side of second tergite; ventral surface of abdomen black with second and third ventrites suffused with yellow; wings with fore half of fore wing deep yellowish brown, the rear half and rear wing much lighter colored. Mexico ....*anomalus* n. sp.

4. Face and front densely bright golden pubescent, also some golden pubescence on thorax and abdomen 5

4. Face and front and abdomen without any golden pubescence; thorax may have slightly golden pubescence, if so the antennae is yellow beneath and posterior orbits have a yellowish band 6

5. Face and front, densely golden pubescent, some on thorax but none on abdomen; posterior three-fourths of pronotum a deep red, with silvery pubescence which appears slightly golden in reflected light; mesonotum and scutellum a deep red with no pubescence; a broad spot above middle coxae, the outer posterior corners of propodeum and the anterior corners of propodeum with brilliant shining silvery (slightly golden) appressed pubescence; the fore part of fore wing back to rear edge of second discoidal cell and covering cubital cells and fore edge of third discoidal and extending to wing tip, a deep brown, the rear of wing and all of rear wing hyaline; the comparison very prominent; exposed part of mentum and fore edge of clypeus red, the latter not much raised above mouth and concave on fore margin; abdomen red, legs black to about middle of femora then reddish; first five joints antennae reddish, last seven black. Mexico ....*aureus* n. sp.

5. Face, head, and thorax densely covered with golden pile and with long pale fulvous hair; head and thorax black; coxae and trochanters black; pronotum black, as is rest of thorax; no large noticeable pubescent spots on thorax; the wings unicolorous; antennae entirely black; clypeus broadly yellow laterally, no yellow on posterior orbits; anterior portion of three or four basal abdominal segments more or less black with short golden pile on apical tergite, the second to fifth segments with a short golden pile at the apex. Panama, Mexico ....*orbiculatus* (Smith)

6. Insect completely rufous except for sternum of thorax, tips of mandibles, some sutures on thorax and base of first tergite, are black, *and* wings deep fuliginous or banded; or body completely rufous with black as above *and* wings light yellow and banded; pronotum angulate behind 7

6. Insect not completely rufous and wings not fuliginous or banded 9

7. Insect rufous as in first part of couplet 4 *and* with deeply fuliginous wings; clypeus much raised above mouth parts, an indication of a tooth in front margin and concave each side of it; first two joints of antennae reddish, last 11 joints yellowish underneath, black on dorsal surface; first recurrent vein received by second cubital cell at apical third. Mexico .... *rubrus* n. sp.

7. Wings banded, with a dark band over basal veins, one over base of marginal cell and backward to rear of wing, and one on apex of wing beyond third cubital cell; wings yellowish between the bands 8

8. Insect rufous all over; only with very little black color on dorsal part of base of propodeum; no hairs on femora and no hairs on head or dorsum of thorax; head slightly longer than broad (42:40); clypeus about 2.3 as broad as long; ratio of lengths of third and fourth antennal joints is 18:16; upper interocular distance slightly less than lower (20:22); a broad dark band over basal and transverse veins, a second one from base of marginal cell through all of second cubital and base of third cubital and across apical three-fourths of third discoidal cell; clypeus hardly raised, truncate and with a slight rim; first two joints antennae reddish, rest brown beneath and black above; first recurrent vein received by second cubital cell just before middle. U.S. and Mexico .... *apache* Banks

8. Insect not rufous all over, at least ventral surface of thorax black; head broader than long; ratios of various measurements different than in *apache;* apex of propodeum as well as sutures on side of thorax black, more black on base of propodeum; black upright hair on front, vertex and dorsal surface of scutellum and postscutellum, hair on rest of body yellow; first two joints of antennae red above and below, rest of dorsal surface deep black or with the fifth and sixth joints yellow. Mexico .... *hurdi* n. sp.

9. Body all black, at most with a slight reddish streak on anterior orbits; wings light yellow. 10

9. Body not all black, either with maculations or some red color; wings generally more hyaline 14

10. Antennae, except tips, legs, and tip of abdomen fulvous; body fuscoferruginous; wings yellowish hyaline; apex of fore wings fuscous and a cloud between the middle and apex fuscous. Cuba .... *nubeculatus* (Cresson)

10. Antennae wholly black, or with basal joints to four or six yellowish and rest of antennae black; no band in fore wings 11

11. A reddish streak on anterior orbits; very hairy on head and thorax, and long hair beneath fore femora, some on mid femora above; first joint of antennae long haired; subdiscoidal vein in rear wing much apicad of cubitus; antennae black; pronotum angulate behind. Mexico .... *rogersi* Dreisbach

11. No marks on anterior orbits; not quite so hairy, less hair or none on

face and middle femora; no long hair on first antennal joint; subdiscoidal vein in rear wing only slightly apicad of cubitus; antennae black or partly yellow; pronotum transverse behind 12

12. Antennae black to apical fourth of third joint, yellow from there to apex joint 7, then black to apex; a broad flange (wide tooth) in middle of front margin of clypeus, slightly concave each side, a narrow rim on clypeus; thorax almost free of hair, only a very few short hairs under fore femora; third antennal joint 1.2 as long as fourth; posterior tibiae with very broad teeth on inner margin, very small ones on the outer margin; glistening between the teeth. Mexico ....*opacus* n. sp.

12. Antennae wholly black or with joints 4-6 yellow; no tooth on front of clypeus 13

13. Antennae wholly black or with joints 4-6 yellow; clypeus slightly concave across front, a rim on front edge of clypeus; thorax very hairy; fore and middle femora more hairy; third antennal joint 1.1 as long as fourth; although this species is larger than preceding, the teeth on inner margin of posterior tibiae only about 0.5 as broad and opaque between teeth. Mexico ....*niger* n. sp.

13. Antennae wholly black, pruinose; clypeus and face below antennae densely covered with a silvery pile; clypeus elongate, obliquely narrowed toward apex, which is subtransverse; mandibles elongate, shining, apex piceous; two round spots of silvery pubescence at apex of propodeum; abdomen shining, pruinose, apical segment thickly clothed with blackish hairs, those at apex being rufous; wings hyaline, broadly violaceous at apex. Guatemala ....*guatemalensis* (Cameron)

14. Head and thorax with golden pubescence; head black with yellow maculations, thorax black (neck may have yellow streak) with only the yellow, appressed pile; abdomen ferruginous or black with yellow and reddish maculations; wings flavo-hyaline, veins yellowish 15

14. Head and thorax without golden pile, thorax and abdomen different 18

15. Abdomen black, maculated as follows: two preapical spots on sides of first tergite, a large spot each side in middle of second tergite, two smaller linear spots on sides of third tergite, two spots about same size on sides of fourth tergite, yellow; the apex of first four tergites rufous and the last two tergites as well as last two sternites completely rufous; the first four sternites with posterior edges rufous; most of mandibles, a large spot each side of clypeus, face, broad anterior orbits, a spot in upper posterior orbits and narrow line on neck, yellow; antennae entirely black; coxae and trochanters black; rest of legs reddish except last joint fore tarsi, last three joints middle tarsi, and last four joints of posterior tarsi black or blackish; clypeus with a small tooth in middle, slightly concave each side, a narrow rim on apex; large teeth on posterior tarsi. Costa Rica ....*ornamentatus* n. sp.

15. Abdomen ferruginous; coxae black, most of rest of legs reddish 16

16. A spot each side of clypeus yellow; basal margins of abdominal segments fuscous; third and fourth joints of flagellum yellowish, rest black; wings flavo-hyaline, nervures testaceous; a small species about 12 mm; spines back of teeth on posterior tibiae not twice as long as teeth. Mexico, El Salvador ....*orbiculatus* (Smith)

16. Clypeus completely black; basal margins of abdominal segments not fuscous, completely red; the spines just back of teeth on dorsal edge of posterior tibiae (on both inside and outside edge) twice as long as teeth 17

17. Antennae with the first two joints and base of third red, rest black; wings a strong reddish yellow, veins strongly reddish except subcosta is amber from base to slightly beyond basal vein; sides of face yellowish from base of antennae to eyes, the yellow color continuing on anterior orbits to the fore ocellus, almost as broad on front as on face; mandibles yellowish on basal half black on apical half; in certain light pubescence on face and thorax golden; apex of fore coxae yellow, all trochanters red; legs all red except the two apical tarsal joints; a large species 21.5 mm long. Peru .... *semirufus* n. sp.

17. First two and three-fourths of third antennal joints black, apex of third, the fourth, fifth and basal three-fourths of sixth white, rest black; wings hyaline, slightly dusky, veins yellowish in reflected light; face black, anterior orbits from antennae to just before antennae with a whitish line; basal 0.75 of mandibles black, a preapical red streak, the apex black; head and thorax completely black with silvery pubescence; all coxae and trochanters black; basal half of fore femora black, and base of last two pair black, rest of legs all reddish including apical tarsal joints; a smaller species, 13.4 mm. Mexico .... *durangoensis* n. sp.

18. Head, thorax and abdomen mostly black with white or yellow maculations 19

18. The whole body yellowish or at least the abdomen rufous 20

19. The sixth antennal joint entirely, the fourth broadly at apex, and the fifth at base, yellow, the rest of antennae black; mandibles (except at apex), clypeus broadly at side, inner orbits broadly, the outer orbits more narrowly at top and bottom, the edges of pronotum all around (except in middle in front) tegula, a mark in center of mesonotum, middle of scutellum, a mark on post scutellum, two marks on mesopleura behind (the lower one the longer), a mark on lower and anterior end of metapleura, and a large mark on sides of abdominal tergites, yellow; a tooth in middle of front edge of clypeus; ventral surface obscure yellow; wings hyaline, nerves black; head and thorax opaque. Panama .... *neotropicalis* (Cameron)

19. Antennae completely black; mandibles black, clypeus black; anterior orbits narrowly, a spot back of eye on temple, a small spot on anterior corners of neck, preapical posterior border of pronotum (except in center), a spot on posterior center of mesonotum, a band on scutellum, a small spot under posterior wing, a larger spot above middle coxae, a spot on outer posterior corners of propodeum, spots on extreme sides of first four tergites, yellow; legs black, but middle and posterior tibiae yellowish on posterior edge, and some on sides, these parts and tarsi with golden colored spines; a tooth on fore margin of clypeus; head and thorax (particularly thorax) shining, fore part of pronotum and neck bare and shining. Mexico .... *octomaculatus* n. sp.

20. Whole body pale yellowish, pronotum angulate behind 21

20. Head and thorax black or black and maculated, abdomen rufous 22

21. Antennae pale on first and second joints, black beyond; head, thorax and abdomen reddish yellow, legs and palpi also, but tarsi darker; fore wings rather yellowish in the cells, veins dark and bordered with dark or smoky, broadly so at basal vein and a broad dark cloud over most of marginal cell and back into apical part of third discoidal cell, wing tip smoky, hind wing also yellowish, tip smoky; head, thorax, coxae, venter and three apical segments with rather long fine hair; some

appressed golden hair on head; both recurrent veins meet their cell at about middle. West Indies ....*monticolus* (Banks)

21. Antennae mostly pale yellowish, but last six joints pale brown; a dark stripe above antennae each side reaching up to ocelli; a narrow black line from eye to eye; mesonotum with a broad median black mark, not reaching hind border, each side a broad black stripe from wing base forward and connected to each other behind, thus leaving a pale U in middle; scutellum with a black spot in middle of base, black behind, postscutellum yellowish across frontal part; propodeum with a large black streak each side leaving only a narrow pale median line, the dark sides narrower behind; pleura entirely pale; wings mostly hyaline, fore wings with a pale brown costal streak beyond basal vein and covering marginal, first, second, and most of third cubital cells and beyond to wing tip. Colombia ....*bequaerti* (Banks)

22. Head and thorax with pale yellow or creamy white spots; clypeus, a broad streak on anterior orbits not touching clypeus, a streak on posterior orbits, an elongate spot on each side of hind margin of pronotum and the lower margin broadly and almost touching side spot of hind margin, a median spot behind on mesonotum, a small spot on scutellum, a larger one on postscutellum; one on outer side of fore coxae and several on sides of thorax, pale yellow or creamy white; petiole of abdomen and fore femora black except rufous on tip; mid and hind femora, all of tibiae, and basal part of tarsi pale yellowish, last few tarsal joints jet black; antennae with six or six and one-half joints jet black, five or four and one-half creamy-white, the last joint brown; pronotum angulate behind. Trinidad ....*ornatus* (Banks)

22. Thorax not maculated and otherwise not as above 23

23. Coxae, trochanter and femora, except apex, black; apex of femora and rest of legs reddish, except last two tarsal joints of fore legs and last three tarsal joints of middle and posterior legs, black; head and particularly the thorax strongly silvery, sericeous with prostrate, glistening pubescence; clypeus slightly concave in front, with a rather broad, preapical rim, which forms a slight trough (concave), particularly on the side pieces; mandibles (except tip and lower edges), sides of face, rather broad anterior orbits to lateral ocelli, and a small spot on posterior orbits just below temples, white; antennae with first two and basal three-fourths of third joints black, apex of third and joints four and five, and base of six underneath, white; third joint of antennae not as long as fourth; lower interocular distance 1.3 times the upper; thorax especially shaggy, long haired, hairs light colored. Panama, Colombia ....*sericeus* n. sp.

23. Legs all red, except coxae and trochanter are mostly black, and last tarsal joints blackish; body not silvery sericeous; clypeus with an indication of a broad tooth in middle of front and slightly concave each side, a preapical rim on anterior edge of clypeus; thorax slightly silvery, slightly bluish; first two joints antennae black, apex of third and all of fourth and fifth bright yellow, rest of antennae black; sides of clypeus at base, fairly wide anterior orbits from clypeus to lateral ocelli, a linear spot on posterior orbits just below temples, most of mandibles and all mentum, reddish; pronotum deep red; wings light yellow; teeth on posterior tibiae very small; a small species about 14.5 mm long. Ecuador ....*caesius* n. sp.

Specificity and Speciation in the Genus Cyrtosomum (Nematoda: Atractidae)[1]

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Four species are known in the atractid genus *Cyrtosomum* Gedoelst, 1919: *C. scelopori* Gedoelst, 1919; *C. penneri* Gambino, 1957; *C. readi* Gambino, 1958; and *C. heynemani* Gambino, 1958. Members of this genus of pinworms are found exclusively in the lizard family Iguanidae. They are apparently further restricted within that family to the North and Central American forms, judging from collecting records available (Pereira, 1935; Karve, 1938; Lent and Freitas, 1948).

Of the 765 specimens of iguanids examined for *Cyrtosomum spp.*, approximately 17 percent or 132, were infected. These infections were distributed as follows: *C. penneri* in 48 lizards (Table I), *C. heynemani* in 36 (Tables II and V), *C. readi* in 25 (Tables III and V), *C. scelopori* in 18 (Table IV). Dual infections of *C. heynemani* and *C. readi* (Table V) were found in 5 host specimens. All but one of the North and Central American genera of iguanids commonly recognized were represented, a total of 46 species and subspecies having been examined.

Among these hosts, *C. penneri* was found in 7 species, *C. heynemani* and *C. readi* in 5, and *C. scelopori* in 6. A single species was found with the dual infection. Table VI lists the 17 species which were found to be uninfected.

With the few exceptions shown in Table V, each species of parasite is specific for several closely related host species. The restriction of each of these nematodes to groups which are closely related taxonomically attests to the high degree of host-parasite specificity exhibited by the genus *Cyrtosomum*. The low incidence of dual and cross infections, despite considerable distributional and ecological overlap of the hosts, indicates a specificity that appears to be physiological rather than ecological. This is best illustrated by the material collected in the southern deserts and coastal mountains of California. Examination of over 300 lizards from this limited geographic region revealed neither dual nor cross infections, yet three of the four species of *Cyrtosomum* appear to have foci of infection in this area.

Taxonomic Considerations

The genus *Cyrtosomum* was divided into four distinct species based on evidence derived from adult morphology, variability, host specificity,

[1] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of California, Los Angeles, NR 103-446.

and parasite distribution (Gambino, 1957a, 1957b, 1957c, 1958). This complex of ecological, physiological, and morphological criteria proved to be the most useful indicator of species separation. The most reliable morphological characters were those employing spicule ratios, which showed the least variability and the greatest concordance with other criteria. Characters employed were spicule ratio (Fig. 1); the ratio of the spicule ratio to body length (Fig. 2); and the ratio of the right spicule to body length compared with the ratio of the left spicule to body length (Fig. 3). Less reliable was the ratio of esophagus length to body length (Figs. 4 and 5), as both the esophagus and body length are subject to change due to contraction upon fixation. Since spicule length remains constant at fixation, ratios involving this structure were found to be more reliable than were total body measurements.

Lip papillae patterns and the number of male caudal papillae

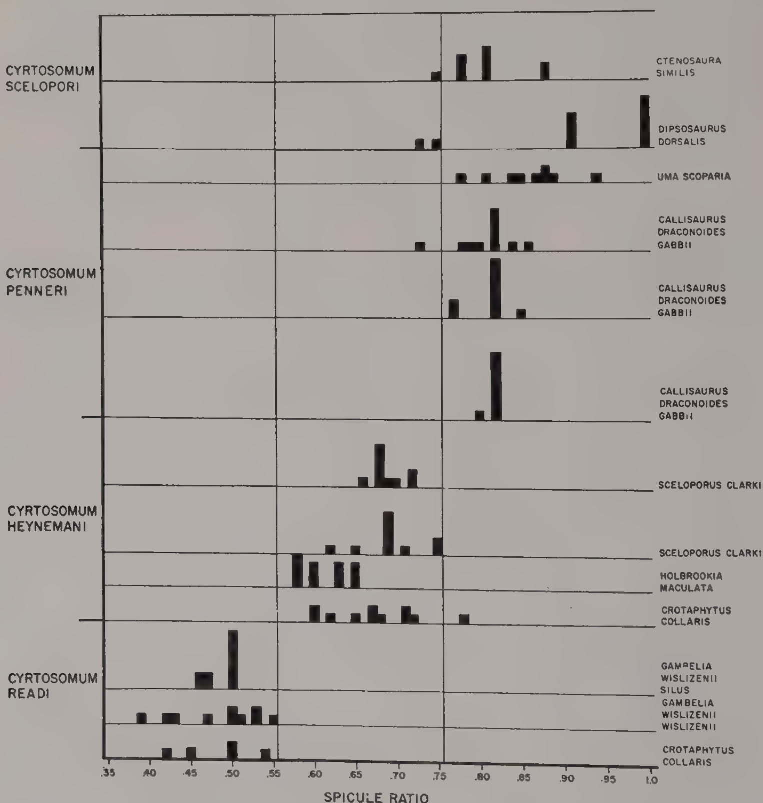

Fig. 1.—Histogram showing the use of the ratio between right and left spicule length as a morphological criterion of speciation in *Cyrtosomum*. Each square represents one specimen.

have been used in previous works in this and related genera and serve to separate *C. scelopori* from the other species in the genus. The latter character, however, is somewhat variable (Fig. 6) and should only be used in conjunction with other criteria.

Biological characters — life cycle, host specificity, and host distribution — gave the additional evidence which warranted division of this genus into four distinct species.

TABLE I.—Incidence and distribution of *Cyrtosomum penneri*

Host	Locality	No. Hosts Examined	No. Infected
Callisaurus draconoides carmenensis Dickerson	San Fransisquito Bay, Baja Calif., Mexico	2	2
C. d. gabbii Cope	Los Angeles Co., Calif.	6	0
	Riverside Co., Calif.	6	2
	San Bernardino Co., Calif.	13	3
	San Diego Co., Calif.	1	1
	Baja Calif., Mexico	34	13
	Sonora, Mexico	1	1
C. d. splendidus Dickerson	Angel de la Guarde Isl., Baja Calif., Mexico	7	5
Petrosaurus sp.	Baja Calif., Mexico	1	1
Sceloporus graciosus vandenburgianus Cope	San Bernardino Co., Calif.	18	2
S. magister rufidorsum Yarrow	Baja Calif., Mexico	1	1
S. occidentalis biseriatus Hallowell	Los Angeles Co., Calif.	74	7
	San Bernardino Co., Calif.	5	0
	San Luis Obispo Co., Calif.	2	0
Uma scoparia Cope	Riverside Co., Calif.	2	2
	San Bernardino Co., Calif.	8	7
Uta stansburiana Baird and Girard	Kern Co., Calif.	1	0
	Los Angeles Co., Calif.	46	1
	San Bernardino Co., Calif.	6	0
	Baja Calif., Mexico	1	0
	Unknown locality	3	0
Totals		238	48

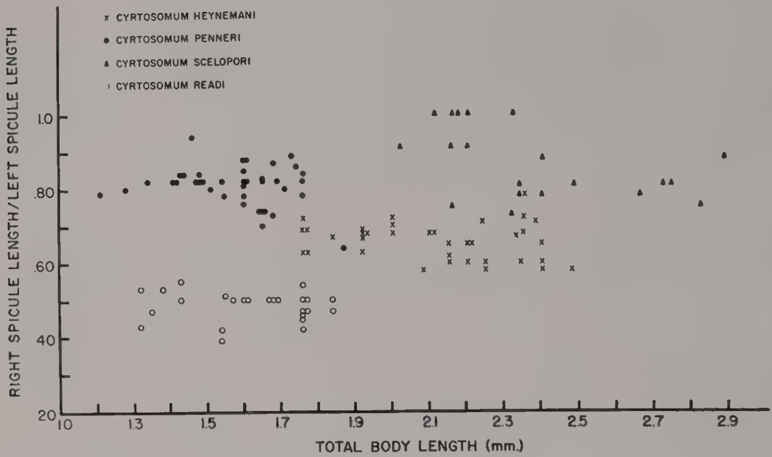

Fig. 2.—Spicule ratio plotted against total body length in *Cyrtosomum* spp.

Zoogeography of Cyrtosomum

C. scelopori has a wider host range and geographic distribution than any of the other species. This form infects *Ctenosaura similis, C. acanthura,*[2] *C. hemilopha, Enyaliosaurus quinquecarinatus,* and *Basiliscus vittatus* throughout the geographic ranges of all of these species, extending from Panama to the southern border of the United States (Fig. 7). In the United States the infection occurs in *Dipsosaurus dorsalis* and *Sauromalus obesus.* The rather limited ranges of these hosts indicate that a disjunct population of *C. scelopori* probably occurs in the United States. The ranges of *D. dorsalis* and *S. obesus* overlap the range of the most northern *Ctenosaura, C. hemophila,* only in Baja California, and there the *C. hemophila* population is an isolated one. *Sceloporus undulatus* is the type host of *Cyrtosomum scelopori,* but it appears that *Cyrtosomum* is only an incidental parasite in this host. Examination of 63 lizards from a wide geographic range revealed only two *Cyrtosomum* infections and these were *C. readi* and *C. heynemani,* not *C. scelopori.*

C. penneri was found in high incidence in three species of hosts: *Callisaurus draconoides, Uma scoparia,* and *Sceloporus occidentalis.* Although infections also occurred in *Sceloporus graciosus, S. magister,* and *Petrosaurus spp.,* too few of these animals were examined to draw conclusions regarding their suitability as hosts of *Cyrtosomum.* The single infection found upon examination of 57 specimens of *Uta stansburiana* indicates that this was an incidental infection. The geographic range of *C. penneri* is an extremely narrow one, extending from the

[2] Reported by Bravo-Hollis, 1942.

deserts and coastal ranges of southern California to Baja California.

Of the two remaining species, *C. readi* has a wider host distribution and a more varied geographic range than has *C. heynemani*. *C. readi* parasitizes *Phrynosoma asio*, a form with a range as far south as the southern states of Mexico, and infects *P. platyrhinos*, *P. m'calli* and *P. solare*, the horned lizards with ranges extending throughout the southwestern United States. *C. readi* also occurs in *Gambelia wislizenii* at the western extreme of its range.

The ranges of *C. readi* and of *C. heynemani* overlap in Arizona and New Mexico. The predominant form in these two states, however, is *C. heynemani*. *C. heynemani* occurs in *Holbrookia maculata*, *Sce-*

TABLE II.—Incidence and distribution of *Cyrtosomum heynemani*

Host	Locality	No. Hosts Examined	No. In-fected
Holbrookia maculata Girard	Apache Co., Ariz.	1	0
	Cochise Co., Ariz.	2	1
	Navajo Co., Ariz.	4	3
	Pima Co., Ariz.	2	0
	Santa Cruz Co., Ariz.	8	7
	El Paso Co., Colo.	1	1
	Guadalupe Co., Mex.	2	0
	Otero Co., N. Mex.	3	1
	Socorro Co., N. Mex.	11	9
	Torrance Co., N. Mex.	1	1
	Tom Green Co., Texas	4	0
	Sonora, Mexico	4	0
	Chihuahua, Mexico	1	0
	Unknown locality	4	0
H. texana (Troschel)	Yuma Co., Ariz.	3	0
	Otero Co., N. Mex.	3	0
	Socorro Co., N. Mex.	28	2
	Tom Green Co., Texas	5	0
Sceloporus clarki Baird and Girard	Greenbee Co., Ariz.	1	1
	Santa Cruz Co., Ariz.	1	0
	Sierra Co., N. Mex.	2	0
	Sonora, Mexico	2	0
	Unknown locality	5	5
S. poinsetti Baird and Girard	Catron Co., N. Mex.	8	0
	Eddy Co., N. Mex.	5	1
	Socorro Co., N. Mex.	2	0
	Chihuahua, Mexico	10	0
S. woodi Stejneger	Broward Co., Florida	1	0
	Highland Co., Florida	6	1
Totals		132	33

loporus clarki, and *Crotaphytus collaris. Holbrookia texana, Sceloporus poinsettii,* and *Sceloporus undulatus* do not appear to be optimal hosts for *C. heynemani,* in view of the low incidence with this form.

Crotaphytus collaris affords a special case in which no barrier to either *C. readi* or *C. heynemani* appears to exist. An explanation for the source of the dual infections might be found in the lizard-eating habit of *C. collaris,* which may, therefore, represent a new host to which these parasites have secondarily become adapted. *C. collaris* occupies a wide geographic range which overlaps that of both parasites *C. readi* in California and *C. heynemani* in New Mexico. In California, a single infection of *C. readi* was reported. In New Mexico, one infection of *C. heynemani* and five dual infections involving these two species were examined, as previously noted.

Few examinations were made of Iguanidae from the eastern parts of the United States. No conclusions therefore can be drawn from the single infection of *C. heynemani* in *Sceloporus woodi* from Florida. Whether or not this represents a disjunct population of *Cyrtosomum* can be learned only from a study of the iguanids which have ranges extending across the southern and southeastern states.

PHYLOGENY OF CYRTOSOMUM

Three criteria considered indicative of increased specialization in *Cyrtosomum* include: reduction in the number of lip papillae, reduction in the number of caudal papillae, and reduction in the number

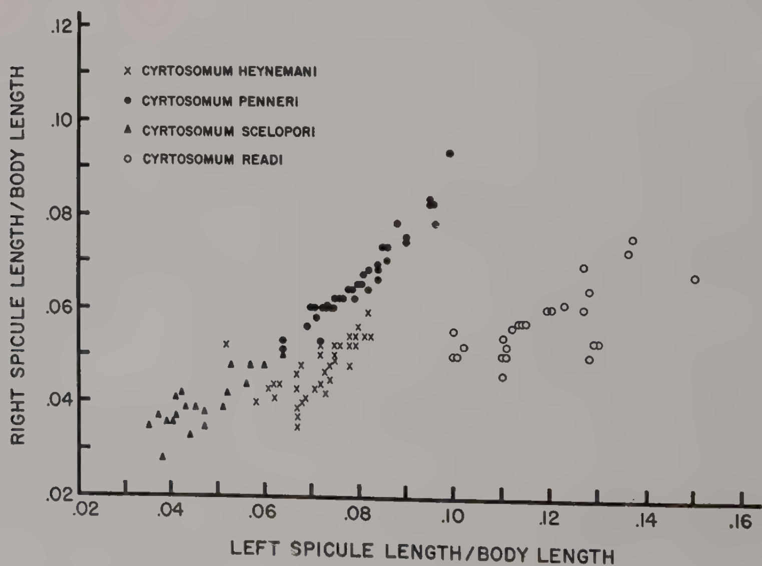

Fig. 3.—Right spicule ratio plotted against left spicule ratio in *Cyrtosomum* spp.

of host species. These criteria were used in this manner by Hetherington 1923; Thapar, 1925; Schuurmans Stekhoven, 1936; Chitwood and Chitwood, 1937; Filipjev and Stekhoven, 1941; Cameron, 1952, 1956; and Chabaud, 1954. According to these authors the reduction of sensory papillae in nematodes occurs concomitantly with increased specialization. Their view is based largely upon the nerves innervating these papillae, which persist despite the loss of the papillae themselves in the course of evolution.

Another indication that the loss of papillae is correlated with in-

TABLE III.—Incidence and distribution of *Cyrtosomum readi*

Host	Locality	No. Hosts Examined	No. Infected
Gambelia wislizenii silus Stejneger	Kern Co., Calif.	10	7
	San Bernardino Co., Calif.	2	0
G. w. wislizenii Baird and Girard	Coconino Co., Ariz.	1	0
	Imperial Co., Calif.	1	1
	Los Angeles Co., Calif.	21	4
	Riverside Co., Calif.	1	0
	San Bernardino Co., Calif.	7	1
	San Diego Co., Calif.	2	0
	Clark Co., Nev.	15	0
	Lyon Co., Nev.	1	1
	Socorro Co., N. Mex.	8	0
	Baja Calif., Mexico	1	1
	Unknown locality	1	0
Phrynosoma asio Cope	Mexico	2	1
P. m'calli Hallowell	Imperial Co., Calif.	1	0
	Riverside Co., Calif.	5	1
	San Diego Co., Calif.	2	0
P. platyrhinos Girard	Inyo Co., Calif.	2	2
	Kern Co., Calif.	1	1
	San Diego Co., Calif.	2	0
	Clark Co., Nev.	1	0
	Washoe Co., Nev.	1	0
P. solare Gray	Maricopa Co., Ariz.	1	0
	Pima Co., Ariz.	2	2
	Yavapai Co., Ariz.	1	1
	Sonora, Mexico	1	0
Totals		93	23

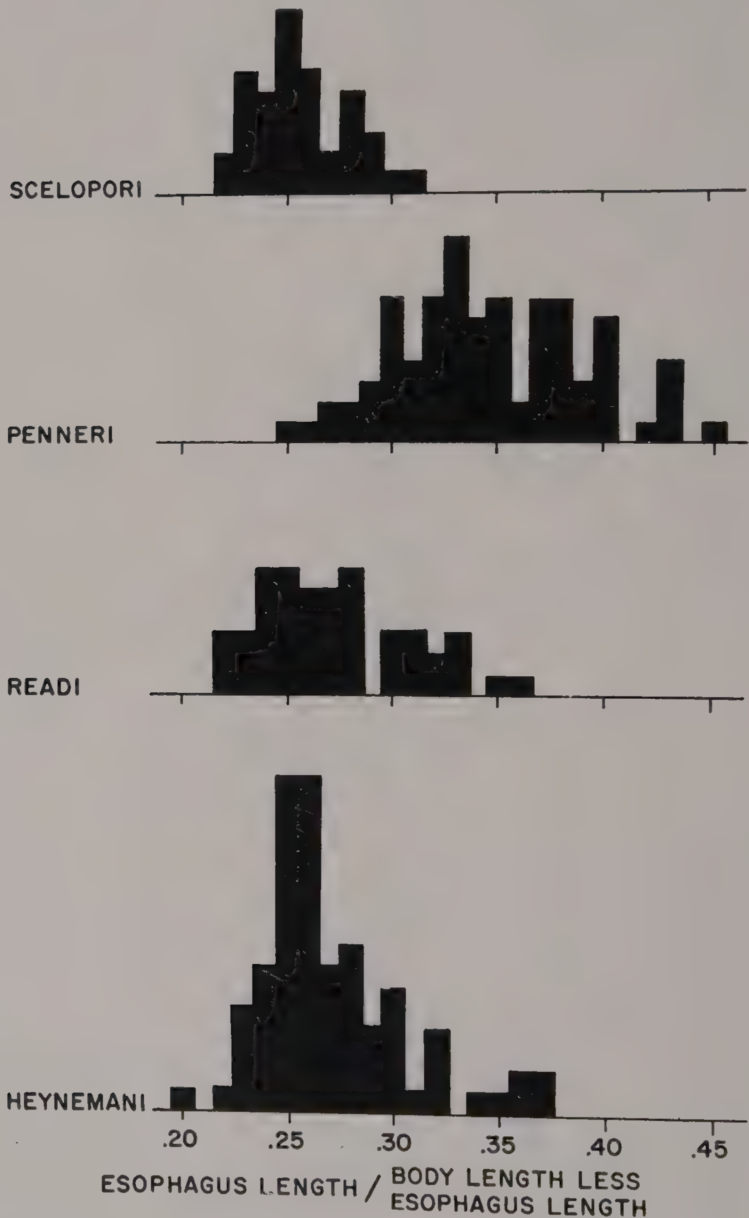

Fig. 4.—Histogram of esophagus-body ratio for each of the four species of *Cyrtosomum*.

creased specialization is found in a study of juvenile stages of the worms. Thapar (1925) reported the presence of certain caudal papillae in juvenile stages which are lacking in full mature adult stages of the same worm. Similar observations were made by one of the authors (Gambino) while studying the life cycle stages of *C. penneri.*

C. scelopori has 7 to 10 pairs of caudal papillae (Fig. 6, F), while *C. penneri, C. heynemani,* and *C. readi* all have either 6 or 7 pairs (Fig. 6). If this character were selected as a measure of divergence from a hypothetical ancestor, *C. scelopori,* which has the greatest number of caudal papillae, would be considered closest to the ancestral stem. The greater number of lip papillae in *C. scelopori* (see Plate II, Fig. F, Gambino, 1957a) can be considered additional evidence for this evolutionary position.

TABLE IV.—Incidence and distribution of *Cyrtosomum scelopori*

Host	Locality	No. Hosts Examined	No. Infected
Basiliscus vittatus Wiegmann	? Mexico	3	0
	Guerrero, Mexico	1	0
	Tierra Colorado, Mexico	3	0
	Vera Cruz, Mexico	2	1
	Zelaya, Nicaragua	1	0
	Panama	3	1
Ctenosaura hemilopha Cope	Sonora, Mexico	2	1
C. s. similis (Gray)	Managua, Nicaragua	2	1
Dipsosaurus d. dorsalis (Baird and Girard)	Mohave Co., Ariz.	4	0
	Inyo Co., Calif.	1	0
	Riverside Co., Calif.	15	4
	Clark Co., Nevada	7	2
	Unknown locality	3	1
Enyaliosaurus quinquecarinatus (Gray)	Oaxaca, Mexico	5	3
Sauromalus obesus (Baird)	Oatman Co., Ariz.	1	1
	Kern Co., Calif.	3	1
	Los Angeles Co., Calif.	1	1
	Riverside Co., Calif.	2	1
	San Bernardino Co., Calif.	4	0
	Clark Co., Nevada	1	0
Totals		64	18

Of the three remaining species, fully mature specimens of *C. penneri* have the smallest number of caudal papillae (usually 6 pairs) and on this basis represent the greatest divergence from the main stem, presumably being the most recently evolved (Fig. 6, B, C, E). Rarely, mature specimens of *C. penneri* possess 7 pairs of caudal papillae (Fig. 6, A). On the other hand, in both *C. readi* and *C. heynemani*, although 7 pairs is the usual number (Fig. 6, G, I), individuals with 6 pairs occasionally occur (Fig. 6, D. H). *C. heynemani*, more often than *C. readi*, possesses the reduced number and is therefore considered closer to *C. penneri*. *C. heynemani*, with a spicule ratio approaching that of *C. penneri* (Fig. 1), and on occasion having the same number of caudal papillae, is often difficult to distinguish from the latter species.

The following sequence, then, represents the divergence from a base form within the genus *Cyrtosomum*, measured in terms of male caudal papillae: *C. scelopori*, *C. readi*, *C. heynemani*, and *C. penneri*.

CORRELATION WITH HOST EVOLUTION

C. penneri and *C. heynemani* occur in the fence lizard genus *Sceloporus*, and in the sand lizards *Uma*, *Callisaurus*, and *Holbrookia*, forms which are among the most recent iguanids (Mittleman, 1942; Savage, 1958). This conclusion seems to be corroborated by the presence of *C. penneri*, considered on morphological grounds to be the most specialized and recently evolved *Cyrtosomum*, in the genera *Uma* and *Callisaurus*, considered by the above authors as the most recent iguanids.

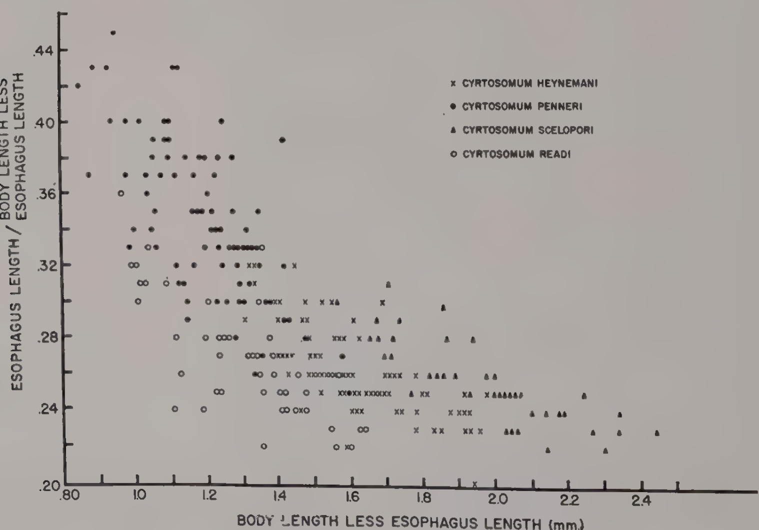

Fig. 5.—Esophagus-body ratio plotted against body length less esophagus length in *Cyrtosomum* spp.

C. readi, which appears to be an early branch of the *C. scelopori* line, is found in the genera *Gambelia, Crotaphytus,* and *Phrynosoma.* The first two genera have been synonymized by some students of the Iguanidae and are considered to have diverged from the main iguanid line extremely early in their evolutionary history. *Phrynosoma* also apparently diverged early from the main line of the Iguanidae, although its exact relationship within the family is somewhat obscure. Evidence of a relationship among these iguanid genera is suggested by their common pinworm parasite.

It appears significant that *C. scelopori,* which occupies the largest number of hosts and covers the widest geographic range, also possesses morphological characters generally considered to be primitive. Furthermore, its hosts are considered by other workers (Mittleman, 1942; Savage, 1958) to be the most primitive iguanids. Both of these lines of evidence therefore suggest that *C. scelopori* most nearly represents the

TABLE V.—Incidence and distribution of dual-infections (*Cyrtosomum readi* and *C. heynemani*) and cross-infections

Host	Locality	Number Hosts Examined	Number Infections	Parasite Species
Crotaphytus collaris Say	Navajo Co., Ariz.	1	0	---- ---- ----
	San Bernardino Co. Calif.	2	1	*C. readi*
	Guadalupe Co., N. Mex.	1	0	---- ---- ----
	Lincoln Co., N. Mex.	2	1	dual
	Otero Co., N. Mex.	1	1	*C. heynemani*
	San Miguel Co., N. Mex.	1	1	dual
	Sierra Co., N. Mex.	1	0	---- ---- ----
	Socorro Co., N. Mex.	8	3	dual
	Torrance Co., N. Mex.	1	0	---- ---- ----
	Eastland Co., Texas	3	0	---- ---- ----
	Terrell Co., Texas	1	1	*C. heynemani*
Sceloporus undulatus (Daudin)	Fulton Co., Georgia	1	0	---- ---- ----
	Bernallilio Co., N. Mex.	1	0	---- ---- ----
	Catrone Co., N. Mex.	5	0	---- ---- ----
	Eddy Co., N. Mex.	2	1	*C. readi*
	Otero Co., N. Mex.	1	0	---- ---- ----
	San Miguel Co., N. Mex.	5	0	---- ---- ----
	Socorro Co., N. Mex.	18	1	*C. heynemani*
	Torrance Co., N. Mex.	14	0	---- ---- ----
	Union Co., N. Mex.	1	0	---- ---- ----
	Washington Co., Utah	10	0	---- ---- ----
	Norfolk Co., Virginia	4	0	---- ---- ----
	Totals	84	10	

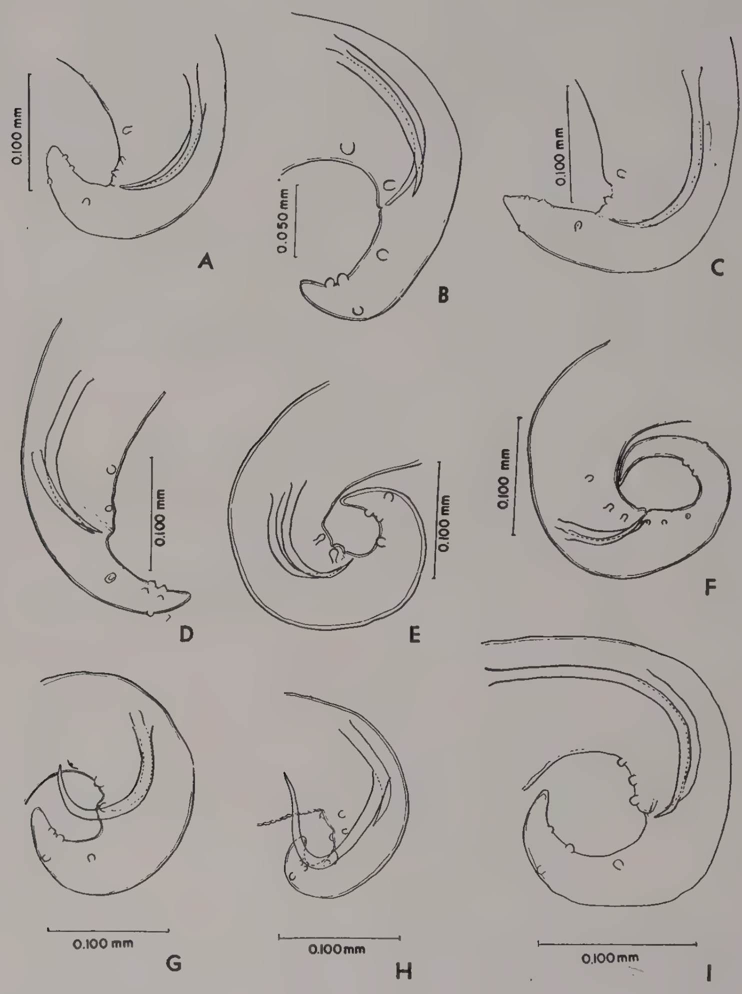

Fig. 6.—Male caudal regions of *Cyrtosomum* spp. A.—*Cyrtosomum penneri* Gambino, 1957, from *Callisaurus draconoides gabbii* Cope. B.—*C. penneri* Gambino, 1957, from *Callisaurus d. splendidus* Dickerson. C.—*C. penneri* Gambino, 1957, from *Uma scoparia* Cope. D.—*C. heynemani* Gambino, 1958, from *Crotaphytus collaris* Say. E.—*C. penneri* Gambino, 1957, from *Uta stansburiana* Baird and Girard. F.—*C. scelopori* Godoelst, 1919, from *Sauromalus obesus* (Baird). G.—*C. heynemani* Gambino, 1958, from *Holbrookia texana* (Troschel). H.—*C. readi* Gambino, 1958, from *Sceloporus undulatus* (Daudin). I.—*C. readi* Gambino, 1958, from *Phrynosoma platyrhinos* Girard.

ancestral type within the genus, and has therefore remained relatively unchanged during the course of evolution of the other members of the genus. In contrast, the other species, *C. readi, C. heynemani,* and *C. penneri,* in that order, appear to represent more recent and specialized offshoots of the *C. scelopori* line.

In view of the lack of information on other characters which might show phylogenetic relationship, it appears unwise at this time to sug-

TABLE VI.—Forms examined and found negative for *Cyrtosomum* spp.

Host	Locality	No. Hosts Examined
Anolis carolinensis Voigt	from Biological Supply Co.	60
Callisaurus draconoides inusitatus Dickerson	Sonora, Mexico	9
Iguana iguana (Linnaeus)	from Biological Supply Co.	10
Phrynosoma cornutum (Harlan)	San Miguel Co., N. Mex.	1
	Socorro Co., N. Mex.	2
P. modestum Girard	Socorro Co., N. Mex.	5
	Brewster Co., Texas	1
Sceloporus magister magister Hallowell	Santa Cruz Co., Ariz.	1
	Kern Co., Calif.	1
	Los Angeles Co., Calif.	6
	San Bernardino Co., Calif.	1
	Socorro Co., N. Mex.	2
S. o. orcutti Stejneger	Riverside Co., Calif.	8
S. scalaris sleveni Smith	Chihuahua, Mexico	1
S. torquata Wiegmann	Amecameca, Mexico	9
	Durango, Mexico	1
S. v. variabilis Wiegmann	Oaxaca, Mexico	1
Streptosaurus mearnsi (Stejneger)	Riverside Co., Calif.	2
Urosaurus auricularis (Cope)	Socorro Isl. Revillagigedo Archipelago, Mexico	8
U. bicarinatus (Dumeril)	Tierra Colorado, Mexico	4
U. microscutatus (Van Denburgh)	San Diego Co., Calif.	4
	Baja Calif., Mexico	2
U. ornatus chiricahue (Mittleman)	Cochise Co., Ariz.	4
U. o. symmetricus (Baird)	Riverside Co., Calif.	1
	Clark Co., Nevada	2
Uta graciosus (Hallowell)	Baja Calif., Mexico	1
Totals		154

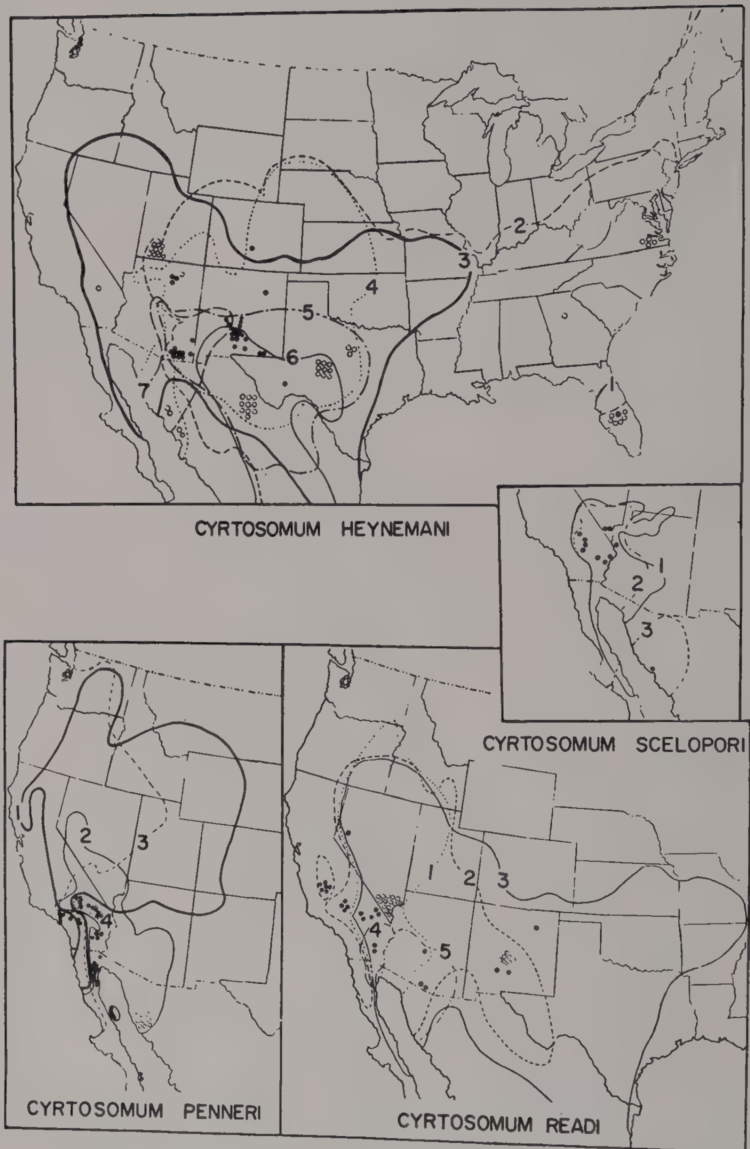

Fig. 7.—Geographic distribution of *Cyrtosomum* spp. and their hosts. The host ranges are numbered to correspond with the species listed below. Infected individuals are indicated by filled circles. Open circles represent uninfected individuals that mark the limits of the collecting range. *Cyrtosomum heynemani* Gambino, 1958: 1. *Sceloporus woodi;* 2. *Sceloporus undulatus;* 3. *Crotaphytus collaris;* 4. *Holbrookia maculata;* 5. *Holbrookia texana;* 6. *Sceloporus poinset-*

gest an exact phylogeny. It seems justifiable, however, to suggest a general sequence of speciation, utilizing those structures which have evolutionary significance according to most students of parasitic nematodes, especially when these criteria can be correlated with zoogeographic and ecological data.

In the evolution of specificity in the genus *Cyrtosomum*, a physical separation of the parasites in widely separated hosts appears to have allowed an accumulation of differences which seem to be physiological ones judging from the collecting data. Assuming this to be the case, the parasites would then become less capable of surviving in other hosts, even in closely related ones. Since the genus *Cyrtosomum* is confined to the Iguanidae, it may be hypothesized that at some time in the early history of both the Atractidae and the Iguanidae, an ancestral iguanid was parasitized by a form similar to *C. scelopori*. A long association between the parasite and its host would presumably have led to an adaptive physiological adjustment between the two, leading to a degree of dependence of the parasite upon its particular host. As some of the host species separated geographically and became morphologically distinct, the parasites accompanying them ultimately did the same. The morphological changes in these parasites appeared as minor cuticular modifications — nematodes being an unusually conservative group in terms of gross morphological changes in evolution. Parallel evolution of the parasite and host presumably maintained the specificity. Some of the host species, on the other hand, appear by their parasites to have diverged less markedly, or perhaps the intestinal environment available to their pinworm parasites remained more uniform. The ancestral species of *Cyrtosomum* was therefore able to parasitize these hosts without undergoing extreme modification or developing a high degree of physiological specificity. The more extreme cases of nematode specificity appear to imply a parallel evolution of host and parasite, marked by morphological divergence and increased dependence of the parasite on its host species. It does not, however, indicate the duration of this association since the adaptive modifications of the worms would vary with the rate of evolution of their hosts. Furthermore, the physiological aspects of this relationship can only be assumed (as in this example) except where laboratory cross-infectivity experiments are available. A host-parasite specificity which is ecological could be a chance occurrence of very recent origin. One which is physiological *might* be a product of long association and thus indicate a phylogenetic relationship. Speculations on the parallel evolution of host and parasite must always assume that the latter condition exists. This should be recognized as an assumption and should

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tii; 7. *Sceloporus clarki. Cyrtosomum scelopori* Gedoelst, 1919 (full range of hosts not illustrated): 1. *Sauromalus obesus;* 2. *Dipsosaurus dorsalis;* 3. *Ctenosaura hemilopha. Cyrtosomum penneri* Gambino, 1957: 1. *Sceloporus graciosus;* 2. *Callisaurus draconoides;* 3. *Sceloporus occidentalis;* 4. *Uma scoparia. Cyrtosomum readi* Gambino, 1958: 1. *Phrynosoma platyrhinos;* 2. *Gambelia wislizenii;* 3. *Crotaphytus collaris;* 4. *Phrynosoma m'calli;* 5. *Phrynosoma solare.*

be a primary consideration to prevent any undue conclusions on host relationships based upon parasite specificity. Failure to recognize this assumption in many works has rendered their conclusions highly questionable and even raised doubts as to the validity of the procedure as a proper tool for the study of phylogeny. These limitations to phylogenetic speculations from host-parasite relations were emphasized by Mayr, Baer, Dubois, Chabaud, and others in their discussions reported in the "First Symposium on host specificity among parasites of Vertebrates" (Baer, 1957). Chabaud (*loc. cit.*: 317) divided specificity into two general types, *recent* and *ancient*. In the former type he placed three degrees, showing increasing specificity: *ecological, physiological,* and *neogenic*. These categories of recent specificity he considered to be independent of the systematic position of the host and hence of no value in evolutionary speculation. The other type of specificity, ancient or primitive specificity, he considered to be of phylogenetic significance. His choice of terms is unfortunate as physiological adaptation could accompany both types of specificity, and would be expected to occur in cases of phylogenetic importance. However, the necessity of distinguishing between accidental or ecological specificity and specificity which is of phylogenetic value is clear. One must look for host relationships from parasite data only in those instances where reasonably good evidence of a physiological genetically-determined dependence on a particular host exists, giving a good probability of parallel evolution. Experimental cross-infectivity tests must always be the ultimate arbiter used to clarify the question of ecological *vs.* phylogenetic specificity.

Several valuable studies have been made which do appear to have application to host phylogeny (Baer, 1947; Cameron, 1952; Clay, 1957; Hopkins, 1949; Rothschild and Clay, 1952). These deal chiefly with the most host specific groups of parasites, such as Mallophaga, Anoplura, certain cestodes, and restricted groups of Nematoda and Monogenea. It seems clear that good phylogenetic evidence from parasites is available, but that each case must be carefully analyzed for alternative explanations.

In the case of nematodes the problem is complicated by the difficulty of specific identification and the possibility of physiological specificity occurring with minimal morphological changes. Hence, it is necessary to depend upon relatively few morphological features, such as the lip or caudal papillary patterns. Nonetheless, these criteria seem to be reliable indices and have therefore been used in the present study.

The more specialized species of *Cyrtosomum* considered in this report are presumably the derived species, more recently evolved and found in more recent host species as well, whereas the least host specific and the least specialized form, found in the most primitive hosts, is considered the oldest parasite species. This contravenes the common assumption that degree of specialization is an index of evolutionary age of a species, and therefore a more specialized, host-specific para-

site would presumably indicate a greater degree of adaptation and a greater age of parasitism. It appears that in this example the primitive host, remaining essentially unchanged, offered a relatively stable and constant environment for its pinworm parasites. No new selective physiological factors acted upon them, and, as with the classic instance of the ancient branchiopod *Lingula,* the same species remained unchanged so long as the environment and the forces of natural selection were unchanged. In the case of parasites which found themselves in more rapidly evolving hosts, different selective pressures were involved. This changing environment would presumably result in the selecting out of new, better adapted variants, specifically adapted to the new host species. Hence, the more specialized and specific parasite species would be the most recently evolved.

SUMMARY

A morphological and distributional analysis was made of the four species of pinworms in the nematode genus *Cyrtosomum.* These are all parasitic in the lizard family Iguanidae and show a marked degree of host specificity which serves as a guide to understanding the evolution in this genus of parasites. The species studied include *Cyrtosomum scelopori* Gedoelst, 1919; *C. penneri* Gambino, 1957; *C. readi* Gambino, 1958; and *C. heynemani* Gambino, 1958. Some 765 iguanid lizards, of 46 species and subspecies, were examined and 17 percent of the individuals were infected. Each parasite was found in 5 to 7 species of hosts and was not found in host species parasitized by other *Cyrtosomum* species except for a few instances of dual infections of *C. heynemani* and *C. readi* in one host species.

Utilizing the morphological criteria of various ratios of spicule to body measurements, the pattern of lip and caudal papillae, and the evidence from parasite distribution and host specificity, the following phylogenetic sequence is proposed: *C. scelopori,* as the oldest, least specialized, and least host specific; *C. readi, C. heynemani,* and *C. penneri,* as more recent successive stages of increased morphological modification and host specificity.

A discussion of the application of such data to the interpretation of host phylogeny is included.

Those species of *Cyrtosomum* which show the greatest morphological change and the maximum host specificity (*C. penneri* and *C. heynemani*) appear to have passed through a more vigorous period of selection in a more rapidly fluctuating environment; (*e.g.*: more rapidly evolving host species) than did the more primitive worms (*C. scelopori* and *C. readi*). These morphological and physiological changes are thought to have occurred despite the fact that the presumably specialized species have not been in their hosts for as long a time as have the worms from which they arose. The latter form, *C. scelopori,* remained in the less rapidly changing environment of its primitive hosts without developing as marked a host specificity or undergoing as apparent a morphological change as did the others.

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Host Relationships of Some Eastern Siphonaptera

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Although the biology of a few species of fleas has been carefully studied because of their importance as vectors of human disease organisms, few detailed studies of host specificity have been made. Since 1952 the senior author and his students at New York State College for Teachers, Albany, in collaboration with the New York State Museum and Science Service, have made intensive collections of fleas in eastern New York. These joint collections have now reached a total in excess of 2000 specimens, parts of which have been previously noted in papers by Sturm (1953), Cummings (1954), Benton, (1955), Benton and Krug (1956), and Connor (1959). In addition to the data on geographical distribution, which will be the subject of another paper, these specimens have provided much-needed information on host-parasite relationships and have clarified several uncertainties as to the "true" or preferred host of certain flea species. These data, along with information from other published and unpublished sources, are sufficient to permit a detailed consideration of host relationships in most of the species involved.

The host relationships of fleas from a world viewpoint have been ably discussed by Hopkins (1958). To be useful to the student of flea-borne diseases, mammalian ecology, and other problems of host-parasite ecology, this work needs to be supplemented by full information on the host distribution of each species. Available information usually falls short of fulfilling the needs of the student of host relationships, and an awarness of the special problems of such studies may help future collectors to make greater contributions to knowledge.

The study of host relationships in fleas is complicated by the fact that these insects, unlike most ectoparasites, are not closely tied to life on the host. Their agility, their leaping ability, and their capacity to survive for long periods of time without food make it possible for them to leave and return to the host many times during a lifetime. Thus accidental associations may occur when fleas leap upon a passing animal other than the usual host. In the Northeast, a single woodland burrow may be occupied, in the course of a few days, by eight to ten different species of rodents and insectivores, so that fleas lying in wait along the burrow or in nest cavities may often reach the wrong host quite by accident.

Accidental associations are also the result of predation. Most of our predators are apparently without specific fleas, although they often carry fleas which belong on their prey animals. Records of fleas from

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predators are therefore generally useless in evaluating host relationship of the parasites.

Another factor which has led to much confusion as to host relationships is the relative abundance of various hosts. For example, *Hystrichopsylla tahavuana,* an apparently rare flea in the northeast, is most often taken from the short-tailed shrew, *Blarina brevicauda.* But this is largely because *Blarina* is taken in such tremendous numbers by mammal collectors. On a proportional basis, this flea is much more common on moles, *Parascalops breweri* and *Condylura cristata,* which are probably the preferred hosts.

There is some evidence, also, that ecological requirements other than the presence of a particular host may be significant in flea distribution. Definite patterns of altitudinal distribution in certain species (e. g. *Orchopeas caedens durus* in New York) are most easily explained on such a basis. The true host, the red squirrel (*Tamiasciurus hudsonicus*) occurs throughout the state, but the flea has thus far been taken only in the Adirondack Mountains.

In spite of these pitfalls, it seems worthwhile at this time to summarize the data on host relationships which can be gained from study of the above mentioned collections. In some cases data from other published and unpublished reports have been used to supplement our data.

This study has been supported by a grant from the Research Foundation of State University of New York. The collections on which

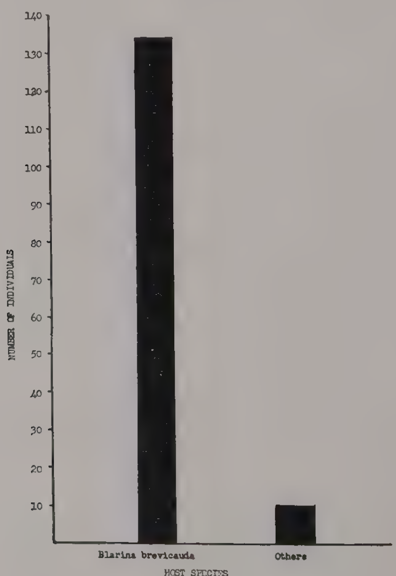

Fig. 1.—Host distribution of 142 specimens of *Doratopsylla blarinae.*

this paper is largely based were made by Paul Connor, Edward Cummings, Arnold Dansky, R. F. Krug, Donald Miller, Daniel Smiley, Robert Sturm and the authors. We are grateful especially to G. H. E. Hopkins, of the British Museum (Natural History) for advice and suggestions from his wide and intimate knowledge of fleas; for critical reading of the manuscript; and for suggesting the classification of host relationships which follows.

A CLASSIFICATION OF HOST RELATIONSHIPS

Since the true biological basis of flea-host relationships is not always apparent, it will be convenient to group the species according to the degree of host specificity which they exhibit. We may place the species in one of five groups, as follows:

Class 1: Species which are obligate parasites of a single host species, although they may occur accidentally on other animals. Such species may often be detected by the fact that their range is coincident with that of the host (Fig. 1).

Class 2: Species which are able to exist as parasites of two or more species of closely related hosts, though showing a definite host preference. Such species often occur on one host in a given area, and upon another host outside the range of the first (Fig. 2).

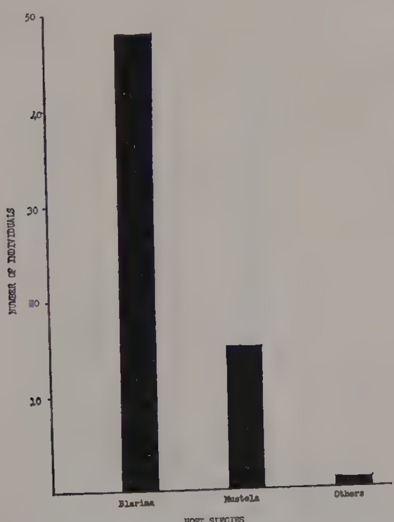

Fig. 2.—Host distribution of 53 specimens of *Nearctopsylla genalis laurentina*.

Class 3: Species which are able to exist as parasites of two or more species and within that group of hosts show little or no host preference. Hosts of the same genus or of closely related genera are often infested by such fleas with no apparent preference being shown in collection data. (Fig. 3).

Class 4: Species which feed on a variety of hosts and are not dependent upon any one species or group, but which nevertheless show a definite preference for a particular species or group (Fig. 4).

Class 5: Species which show no apparent host preference, occurring on a wide variety of unrelated host animals in approximately equal numbers. This does not exclude the possibility that the flea may be limited in host distribution by other factors, such as size of host, type of nest of host, etc. (Fig. 5).

Eventual proof of host associations and relationships must rest upon experimental data, rather than upon deductions from collections. However, the large numbers of specimens at our disposal permit a more accurate appraisal of host relationships than has heretofore been possible.

ACCOUNTS OF SPECIES

The classification which follows includes all the species of fleas

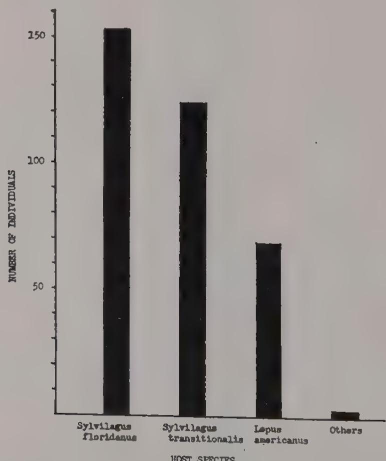

Fig. 3.—Host distribution of 349 specimens of *Cediopsylla simplex*. Greatest number was taken from *Sylvilagus floridanus* because that host was taken in greatest numbers. Number of fleas per host is about equal in all three species of rabbit hosts.

which we have collected in eastern New York. Those species for which the data are few or inconclusive are indicated by an asterisk. Our arrangement of families follows that of Hopkins and Rothschild (1953). The number in parentheses following the host relationship class designation indicates the number of individuals we have collected.

FAMILY PULICIDAE

Cediopsylla simplex (Baker).—This flea is confined to rabbits, although it often occurs upon their predators. In eastern New York it occurs without apparent preference upon all three native species of Leporidae, *Lepus americanus, Sylvilagus floridanus* and *S. transitionalis.* Class 3. (349).

Ctenocephalides canis (Curtis).—Although our single record of the dog flea is insufficient to permit a guess as to host relationships, abundant records from other places indicate that the domesticated dog, *Canis familiaris,* is the preferred host. It is also found on foxes, coyotes, and occasionally on other hosts. Our single record is from the red fox, *Vulpes fulva.* Class 2. (1).

FAMILY HYSTRICHOPSYLLIDAE

**Atyphloceras bishopi* Jordan.—Although widely distributed, this species seems to be difficult to secure, and few records are available. Our records are mostly from *Microtus pennsylvanicus,* but Fuller (1943) secured 27 specimens from *Clethrionomys gapperi.* It is thus quite certainly a parasite of Microtinae, although it is not possible to tell which, if either, of these species is the more frequent host. Class 2 or 3. (20).

**Hystrichopsylla tahavuana* Jordan.—This large flea has been taken in approximately equal numbers in eastern New York on *Parascalops breweri, Condylura cristata* and *Blarina brevicauda.* Because of the large numbers of *Blarina* which are taken, and the small numbers of the moles which fall to the trapper, it seems likely that the moles are preferred hosts. Class 3. (14).

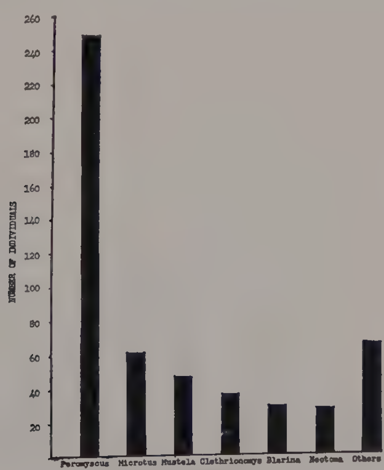

Fig. 4.—Host distribution of 509 specimens of *Epitedia wenmanni.*

**Stenoponia americana* (Baker).—About half of the specimens of this species which have been reported in the literature were taken from deermice (*Peromyscus*), with the rest coming from a wide variety of small mammals. This giant flea is not commonly taken, and further collecting is essential before its host relationships will be clear. Class 4. (27).

**Catallagia borealis* Ewing [= *C. onaga* Jordan].—The only sizable collection of this species was reported by Fuller (1943) from the red-backed mouse, *Clethrionomys gapperi*. It has also been collected several times from *Blarina brevicauda*. Its rarity in collections makes it impossible at present to evaluate its host relationships. Class unknown. (3).

Epidetia wenmanni wenmanni (Rothschild) and *E. w. testor* (Rothschild).—Throughout its wide range, this species is most commonly associated with *Peromyscus*, but it occurs so often on a variety of small mammals that its connection to this genus must not be a very close one (Benton, 1955). Class 4. (41).

**Epitedia faceta* (Rothschild).—Although the red squirrel, *Tamiasciurus hudsonicus*, is the type host of this flea, our records indicate that the flying squirrel, *Glaucomys volans*, is the usual host. Our specimens have been taken in the colder months, indicating that extensive collecting in winter might supply enough specimens to clarify this matter. Class 1 or 2. (24).

Tamiophila grandis (Rothschild).—This large flea is almost never recorded from any host other than the chipmunk, *Tamias striatus*. Relatively few specimens have been taken but its host relationship is clearly apparent. (Class 1. (17).

Ctenophthalmus pseudagyrtes pseudagyrtes Baker.—This is at the same time one of the most common fleas and the least host-specific flea occurring in our area. Fleas found on odd hosts such as skunks, porcupines, or other hosts having no flea fauna of their own are most likely to be of this species. On these hosts it sometimes occurs in considerable numbers. Pine mice, lemming mice, and jumping mice are among the species which have no specific fleas in this area but which often harbor *Ctenophthalmus* in fair numbers. Class 5. (249).

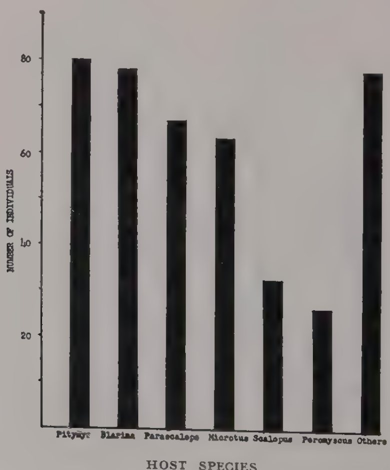

Fig. 5.—Host distribution of 422 specimens of *Ctenophthalmus pseudagyrtes*.

Doratopsylla blarinae C. Fox.—Krug and Benton (1953) collected 46 fleas of this species without recording one from any host other than the short-tailed shrew. This is an indication of its close affinity for this shrew. Occasionally it occurs on other mammals which are ecologically associated with its true host, but even such occurrences are rare. Class 1. (142).

**Corrodopsylla curvata curvata* (Rothschild).—This species is reported by Holland (1949) to be most closely associated with the genus *Sorex,* although it has been reported frequently from *Blarina.* At the present time insufficient numbers are available to permit a conclusion as to its preferences within the shrew family. Class 3. (2).

**Conorhinopsylla stanfordi* Stewart.—The red squirrel, *Tamiasciurus hudsonicus,* is the type host of this seemingly rare flea, and one of our specimens comes from the gray squirrel, *Sciurus carolinensis.* Failure to secure it from large collections of the red squirrel (*e.g.,* Layne, 1954), has led to doubt as to its association with this host. Our collections have been almost exclusively from the flying squirrel, *Glaucomys volans,* and it seems likely that further collections will show this to be the preferred host. Class 2. (20).

Nearctopsylla genalis laurentina Jordan and Rothschild.—Although we have a rather large series of this flea, its host relationships are not entirely clear. The short-tailed shrew is the most frequent host, and we have a fairly large series from weasels, probably the result of predation. It occurs on other shrews, and less commonly on moles, indicating that the class 2 designation is probably the correct one. Class 1 or 2. (53).

Oropsylla arctomys (Baker).—Within our area, this flea occurs only on the woodchuck, *Marmota monax,* but in other sections it occurs on other marmots. Occasional records from rabbits and predators are no doubt accidental. Class 2. (22).

Opisodasys pseudarctomys (Baker). — Although most often taken from *Glaucomys sabrinus,* the northern flying squirrel, this flea is also known to occur in nests and on individuals of *G. volans.* It has been taken in sufficient numbers from both these species to indicate that it can survive as a host of either, though evidently occurring most abundantly on the former. Class 2. (67).

Orchopeas caedens durus (Jordan).—*Orchopeas caedens* is a specific parasite of the red squirrel, *Tamiasciurus hudsonicus.* In the east, however, it does not occur throughout the range of this squirrel, thus presenting a very interesting problem in the causation of flea distribution. It occurs in the Adirondacks, and possibly in the Catskill Mountains as well, although it has not yet been collected there. To the south, and apparently wherever the range of the red squirrel overlaps that of the gray squirrel, *Sciurus carolinensis,* this flea is replaced by *O. howardii.* We have not thus far collected both species of flea from the same squirrel or from the same locality. Class 1. (39).

Orchopeas leucopus (Baker).—This abundant flea occurs with apparent indifference on our two deermice, *Peromyscus leucopus* and *P. maniculatus.* Other occurrences on ecological associates of these mammals are sufficiently uncommon to be considered accidental. Class 3. (456).

Orchopeas sexdentatus pennsylvanicus (Jordan).—A true parasite of the woodrat, *Neotoma magister,* this species occurs wherever this host occurs. It has not been found in regular association with any other species. Class 1. (17).

Orchopeas howardii howardii (Baker).—This flea has a close affiliation with the gray squirrel, *Sciurus carolinensis,* and apparently does not occur to the north of the range of this host (Holland, 1949). Although this evidence would

appear to place it as a Class 1 flea, its occurrence in large numbers on *Glaucomys* and *Tamiasciurus* indicate an ability to survive as a parasite of these squirrels as well. In the south it occurs in large numbers on the fox squirrel, *Sciurus niger*. Class 2. (230).

**Ceratophyllus gallinae* Schrank.—The chicken flea will bite rats and man, as well as various species of domestic poultry, but seems unable to establish itself on any mammal. Our collection of this species, from *Rattus norvegicus,* sheds no light on its true affiliations. Class 2. (1).

Megabothris acerbus (Jordan).—The eastern chipmunk, *Tamias striatus,* is the host of this highly specific flea, which is rarely taken on any other animal. Class 1. (43).

Megabothris asio asio (Baker). — This appears to be a nest flea, and is seldom taken from trapped animals, so that its host distribution is difficult to evaluate. In our area, however, it seems to be a parasite of the meadow vole, *Microtus pennsylvanicus,* from whose nests most of our specimens were taken. Class 1. (27).

**Megabothris quirini* (Rothschild).—Evidence indicates that this species is associated with the red-backed mouse, *Clethrionomys gapperi,* but it has been taken so rarely in our area that its host relationship is not definite. Its apparent rarity may indicate that it, like *M. asio,* is primarily a nest flea. Collectors should examine nests of the red-backed mouse to secure data on this point. Class 1. (11).

Monopsyllus vison (Baker).—This species is a parasite of the red squirrel, and is not known from any location where red squirrels do not occur. Where both red and gray squirrels occur, however, it may be found in some numbers on the gray squirrel (Wells, 1957). Class 1. (17).

Nosopsyllus fasciatus (Bosc).—Because this flea is a parasite of the Old World mice and rats, it has been collected in tremendous numbers in Public Health Surveys. These surveys show it to be found primarily on the Norway rat, *Rattus norvegicus,* the black rat, *Rattus rattus,* and the house mouse, *Mus musculus,* with some apparent preference for the Norway rat. Class 2. (12).

FAMILY LEPTOPSYLLIDAE

Peromyscopsylla catatina (Jordan).—This flea has been taken from several hosts, but evidence from its local distribution in eastern New York indicates that it is a true parasite of the red-backed vole, *Clethrionomys gapperi.* Most of our specimens come from this host, and we have never taken this flea in any area where red-backed voles do not occur. Class 1. (34).

Peromyscopsylla h. hesperomys (Baker).—In our area, this species occurs without apparent preference on *Peromyscus leucopus* and *P. maniculatus.* It occasionally appears on other ecologically associated mammals. Class 3. (188).

**Peromyscopsylla scotti* I. Fox.—Our only specimens of this species are from *Peromyscus leucopus.* They are too few, however, to establish a definite host relationship. This flea appears to be very rare in eastern New York, and extensive collections in the Hudson valley have yielded only one locality record. Possibly competition with *P. hesperomys* is a factor in its distribution, or perhaps it is a nest flea which is seldom found upon the host animal. Class 1 or 2. (4).

FAMILY ISCHNOPSYLLIDAE

Nycteriodopsylla chapini Jordan.—This little known and seldom collected flea has been most often taken from the big brown bat, *Eptesicus fuscus.* Our

collection was from a winter roost, and further examination of such roosts might show this species to be more common than past collections indicate. Class 1. (9).

Myodopsylla insignis (Rothschild).—This is a common parasite of the little brown bat, *Myotis lucifugus,* and occurs in great numbers in breeding colonies. It has, however, been taken from other bats in sufficient numbers to indicate that it is not wholly restricted to this one species. Class 2. (100).

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The Distribution, Variation, and Life History of the Frog Cochranella viridissima in Mexico[1]

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Frogs belonging to the family Centrolenidae first were reported from México by Taylor (1942:74-7), who described *Centrolenella viridissima* from Agua del Obispo, Guerrero, and recorded a specimen of *Centrolenella fleischmanni* from Salto de Agua, Cerro Ovando, Chiapas. An additional specimen of *C. viridissima* was reported by Taylor (1949:12-3) from Río Grande, Oaxaca. Goodnight and Goodnight (1956:146) recorded *C. fleischmanni* from Palenque, Chiapas. Taylor (1951:34) placed both *fleischmanni* and *viridissima* in the genus *Cochranella.*

Field work in México by the senior author in 1956 and by both of us in 1958 has resulted in doubling the number of known specimens of these frogs from that country. Also, life history data were obtained. The purpose of this report is to discuss the variation in, and systematic status of, Mexican centrolenids, to describe the eggs and tadpoles of *C. viridissima,* and to place on record the accumulated locality records for this frog in México.

Acknowledgments.—For the loan of specimens we thank Doris M. Cochran, United States National Museum (USNM);[2] James R. Dixon, College Station, Texas (JRD); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ), and Richard G. Zweifel, American Museum of Natural History (AMNH).

We are indebted to Ann S. Duellman, Richard E. Etheridge, and John Wellman for their assistance in collecting these elusive frogs and to Priscilla H. Starrett for helpful suggestions. The senior author's field work was made possible by grants from the American Philosophical Society, the National Academy of Sciences, and the Graduate School of Wayne State University, and the generous support of the Museum of Zoology of the University of Michigan.

Variation and Systematic Status

Taylor (1942:75) stated in the diagnosis of *C. viridissima:* "Re-

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[1] Contribution No. 46 from the Department of Biology, Wayne State University, Detroit 2, Michigan.

[2] Specimens are cited by catalog number following abbreviations for collections; the private collection of Edward H. Taylor and Hobart M. Smith is abbreviated EHT-HMS.

lated to *C. fleishmanni* [*sic*], but with shorter, stouter limbs and shorter, wider digits; tibiotarsal articulation does not or barely reaches tip of snout while in *fleishmanni* [*sic*] it reaches much beyond." He stated also that in *fleischmanni* the choanae are much larger, there are no fleshy folds below the anus, and the upper parts are smoother. Upon reporting a specimen of *C. viridissima* from Río Grande, Oaxaca, Taylor (1949:13) stated: "*Centrolenella fleischmanni,* also occurring in México, differs in having the second finger much shorter than the first. A white area is present on the eyelids. The leg is distinctly longer, the tibiotarsal joint reaching 2-3 mm beyond the snout tip."

Of six topotypic *viridissima* the tibiotarsal articulation reaches to between the eye and the snout in two, and to the tip of the snout or slightly beyond in four. In 23 *fleischmanni* from Costa Rica (UMMZ 117668-71) the tibiotarsal articulation falls between the anterior corner of the eye and someplace beyond the snout. The relative lengths of the first and second fingers are highly variable in both series. In all, the upper eyelid is white. In specimens of both series there are fleshy folds beside the anus; in some these folds extend below the anus. There is no significant difference in the size of the choanae, nor is there any evident difference in the relative smoothness of the skin on the dorsum.

Nevertheless, there exist certain minor differences between the series of *C. fleischmanni* from Costa Rica and the specimens of *C. viridissima* from Guerrero. In those from Costa Rica the digits of the feet are slightly more robust than those in *viridissima.* All of the *fleischmanni* have scattered chromatophores on the back; these appear in only one of the six topotypes of *viridissima.* In other specimens from México the relative thickness of the digits approximates that in topotypic *viridissima.* About half of the specimens have scattered chromatophores on the dorsum. All Mexican specimens have a silvery white pericardium, which is especially noticeable in living individuals. On the basis of this comparison we tentatively conclude that the existing specimens from México represent a single species, *viridissima,* which we provisionally consider distinct from *fleischmanni* as known in Costa Rica and Nicaragua. Possibly these populations represent a single species or two races of a single species. The exact status of these frogs can be settled only after the acquisition of more specimens, especially from northern Central America, and careful comparison of the living frogs.

Adults of *C. viridissima* from eastern México are slightly larger than those from Agua del Obispo, Guerrero, and show minor differences in proportions of the body (Table I). Because of their poor state of preservation, measurements could not be taken with any degree of accuracy on most of the specimens from Chiapas.

In life these frogs are pale lime green above, sometimes with small scattered cream or pale yellow spots. The feet are yellow, and the vocal sac is white. The skin of the venter is transparent, permitting a view of the silvery white pericardium, of the stomach and intestines, and of the ventral abdominal vein. The iris is light golden (Fig. 1).

TABLE I.—Variation in size and proportions of adult male *Cochranella viridissima* from Veracruz and Guerrero, México (Means are given in parentheses below the observed ranges).

Sample	Number of Specimens	Snout-vent Length	Foot Length / Snout-vent Length	Head Length / Snout-vent Length	Head Width / Snout-vent Length
Veracruz	4	23.9-24.8 (24.5)	.425-.452 (.438)	.243-.251 (.246)	.332-.350 (.341)
Guerrero	5	20.2-21.9 (21.2)	.462-.465 (.464)	.251-.262 (.256)	.347-.366 (.358)

DISTRIBUTION AND ECOLOGY

Recent collecting in México has revealed the presence of *Cochranella viridissima* on the Gulf slopes of the Sierra Madre Oriental as far north as central Veracruz. Also, it has been collected on the Gulf lowlands of Chiapas and in Los Tuxtlas, an isolated volcanic range in southern Veracruz. Thus, the species is known from foothills from central Veracruz and central Guerrero southeastward to the Gulf lowlands of Chiapas and to the Pacific slopes of the Sierra Madre in Oaxaca and Chiapas. Locality records for the 31 Mexican specimens are:

Chiapas: Palenque, UIMNH 11302-3; Río Mala, Unión Juarez, UIMNH 40969; Salto de Agua, Cerro Ovando, USNM 115499; Soconusco, UMMZ 87863. *Guerrero:* Agua del Obispo, EHT-HMS 27719-27 (Taylor, 1942), UMMZ 118584 (6). *Oaxaca:* Cerro Azul, UIMNH 40970; Río Grande, AMNH 51846. *Veracruz:* 3 km. SW of Huatusco, UMMZ 119517; 7 km. ENE of Huatusco, UMMZ 118585; Los Chaneques, 2 km. N of Santiago Tuxtla, UMMZ 115297 (3), 118174 (3); Yanga, JRD 647.

At Los Chaneques in the foothills of Los Tuxtlas these frogs were at an elevation of 350 meters in a small ravine surrounded by remnants of rainforest. Near Huatusco they were at elevations of about 1300 meters along streams in cloud forest on the slopes of the Sierra Madre Oriental. At Agua del Obispo, Guerrero, they were on broad leaf trees along a small stream in open pine-oak forest; this locality lies at an elevation of 900 meters near the crest of a low divide on the Pacific slopes of the Sierra del Sur.

LIFE HISTORY

Breeding choruses of *Cochranella viridissima* have been found on June 28, 1958, at Agua del Obispo, July 17, 1958, near Huatusco, and July 20, 1956 at Los Chaneques. A single male was heard calling at

Los Chaneques on January 25, 1958, and another near Huatusco on January 27, 1958. Males call from leaves of trees over mountain streams. At Agua del Obispo individuals were found 2 to 3 meters above the stream; others were somewhat higher but could not be reached. At Los Chaneques calling males were on leaves of trees overhanging the ravine and small stream; one was on the underside of a vine leaf only about two meters above the water. Near Huatusco they were calling from the tops of trees above rushing mountain streams; at 3 kilometers southwest of Huatusco many frogs were calling from treetops about 20 to 25 meters above the stream. At another locality one was secured from a leaf about 10 meters above the stream.

The call is a single high "peep" usually no more than two or three seconds in duration. Frequently the time-lapse between calls is more than one minute.

At Agua del Obispo, Guerrero, a clutch of 22 eggs was found on June 28, 1958, and another of 29 eggs on July 2, 1958. Both clutches were adherent to the undersides of tree leaves 1 1/2 to 2 meters above the stream. The envelopes of the individual eggs were barely discernible; the entire clutch was covered with jelly (Fig. 1). The jelly was clear, pale green; the yolk was yellow, and the embryos were creamy white. Under magnification, preserved embryos show closely placed chromatophores on the dorsum of the body and on the muscular part of the tail. The embryos showed no particular orientation; some were head down, others, head up. When the leaf was rotated, some

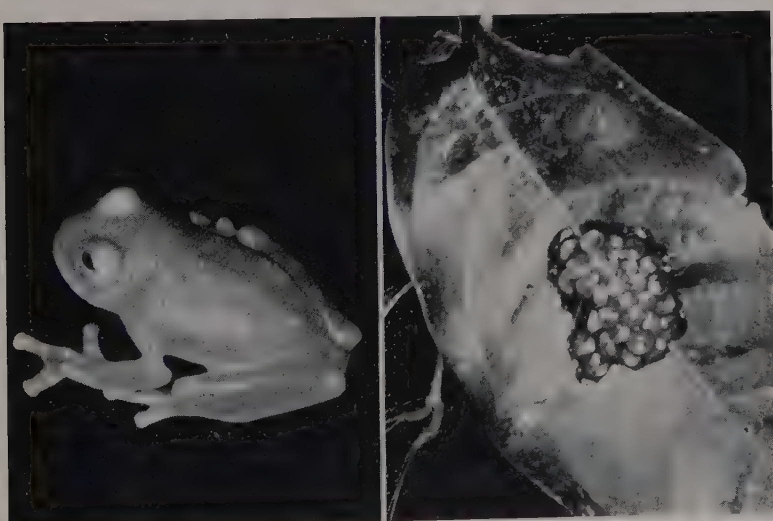

Fig. 1.—Adult and eggs of *Cochranella viridissima* from Agua del Obispo, Guerrero. Left: adult male (approximately twice natural size; actual length 21.9 mm). Right: clutch of eggs on underside of leaf overhanging a stream (approximately one-half natural size).

of the embryos rotated with it, but most retained their original positions.

The leaves with the adherent egg-clutches were collected and suspended above plastic containers. The clutch discovered on June 28 hatched on July 1; that found on July 2 hatched July 6. A hatching tadpole has a body length of 2.9 mm. At the time of hatching, the tadpoles have two partially developed lower tooth rows and the beginning of an upper row.

Two tadpoles six days old have body lengths of 3.1 and 3.4 mm. and total lengths of 10.5 and 11.2 mm. Ten tadpoles eight days old have body lengths from 3.1 to 3.8 (average 3.4) mm and total lengths from 10.4 to 12.6 (average 11.5) mm.

Following is a description of an eight-day old tadpole (UMMZ 118589): In dorsal view the head and body are approximately oval, widest at midbody; eyes one-third distance from snout to end of body and somewhat closer to midline than to lateral outline of head; nostrils midway between eye and snout and somewhat more median than eyes. In lateral aspect, greatest depth of body two-thirds distance from snout to vent; mouth anteroventral; snout protruding beyond mouth; spiracle about three-fourths the distance from snout to vent, below midline, and its opening directed posteriorly; anal tube median and sloping posteroventrally at an angle of about 35 degrees. Tail musculature terminating in a point immediately anterior to tip of tail; greatest depth of tail musculature slightly more than one-half greatest depth of tail; tail fin relatively narrow and rounded posteriorly. In preservative, tail musculature and body pale cream, with scattered chromatophores on dorsal surface; tail fin transparent (Fig. 2).

Tooth rows 2-2; second upper tooth row present only laterally; lower tooth rows slightly longer than upper ones, complete and wavy. Lips only slightly differentiated, edges scalloped, and not forming a distinct sucker. A row of relatively large papillae around mouth; a slight fold of the lips at lateral corners of mouth. Upper horny beak forming a broad arch, not indented medially; lower beak heavier and forming a narrower arch (Fig. 3).

In comparison with tadpoles of *C. fleischmanni* of approximately the same size from Costa Rica (UMMZ 118658), the following differences are noted: *fleischmanni* has a somewhat more blunt snout in lateral view, mouth directed more ventrally, three well-developed lower

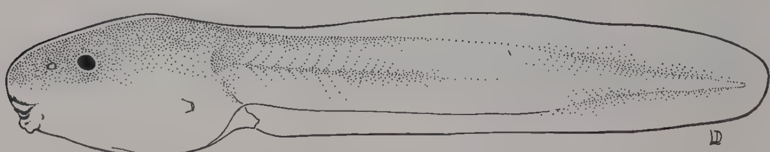

Fig. 2.—Eight-day old tadpole of *Cochranella viridissima* (UMMZ 118589); x 8, actual length 12.6 mm.

Fig. 3.—Mouth parts of eight-day old tadpole of *Cochranella viridissima* (UMMZ 118589); x 50.

tooth rows, and upper beak indented medially. Tadpoles of *C. granulosa* (UMMZ 118660) and *C. talamancae* (UMMZ 118657), both from Costa Rica, differ from *viridissima* in having proportionately longer and narrower bodies, longer tails with narrower fins, mouth large and sucker-like, and upper beak indented medially.

Three metamorphosing individuals were found sitting on herbaceous vegetation along a small stream at Los Chaneques on January 25, 1958. They have snout-vent lengths of 11.6, 12.3 and 12.5 mm. Only a stub of the tail remains on each; the mouth has not completely expanded. In life they were pale green.

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Home Range, Reproduction, and Foods of the Swamp Rabbit in Missouri

J. E. TOLL,[1] T. S. BASKETT,[2] and C. H. CONAWAY[3]

In Missouri, the swamp rabbit (*Sylvilagus aquaticus* (Bachman)) occurs principally in the southeastern lowlands. It is a locally abundant and popular game animal. Relatively little is known of the life history of this species, particularly in the northern part of its range. The object of this study is to contribute to our knowledge of specific aspects of the life history of this species.

The study area was in Mingo swamp which lies in Stoddard, Wayne, and Bollinger counties, in an abandoned valley of the Mississippi River. The swamp formerly supported extensive stands of bald cypress (*Taxodium distichum*), tupelo gum (*Nyssa aquatica*) and several species of oaks. Drainage, logging, and clearing of the higher land for farms have greatly altered the landscape. But large acreages of good swamp rabbit habitat remain in cut-over lowland hardwood types, particularly on the Mingo National Wildlife Refuge and the Duck Creek Wildlife Area.

This paper is a contribution from the Missouri Cooperative Wildlife Research Unit and the Department of Zoology, University of Missouri. The senior author was an Edward K. Love Fellow. We are indebted to Howard M. Wight, Missouri Conservation Commission, for valued suggestions and assistance; and to G. K. Brakhage and L. J. Schoonover for facilities and assistance.

Home Ranges

The trapping area.—Sizes of home ranges were determined both by trapping and by beagle chases. These operations were carried out on a portion of the Duck Creek Wildlife Area. The trapping area comprised 72 acres, extending from the edge of a shallow impoundment on the south to higher dry land on the north (Fig. 1). This was a logged-over hardwood site; pin oaks (*Quercus palustris*) and overcup oaks (*Q. lyrata*) dominated. Overstory trees seven to ten inches dbh were most common. Stand density varied from about 95 overstory trees per acre to openings with only 15 per acre; in these openings there was an undergrowth of blackberries (*Rubus sp.*) and other small shrubs. The north and west sides of the area were bordered by a road with a grassy right-of-way about 70 yards wide.

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Trapping and tagging procedure.—The trapping area was divided into 72 one-acre squares. A trap was placed at the center of each square, making a grid nine traps deep and eight wide; traps were 70 yards apart. Box traps operated with a treadle were used. Various types of bait were used, but unbaited traps were as successful as baited ones.

Trapped rabbits were weighed, sexed, measured, tagged, and released at the point of capture. Recaptured rabbits were recorded and released.

Two types of tags were used. One was a small numbered aluminum poultry tag attached to the ear with crimping pliers. Cottontails (*Sylvilagus floridanus*) were marked with this tag only. The alumi-

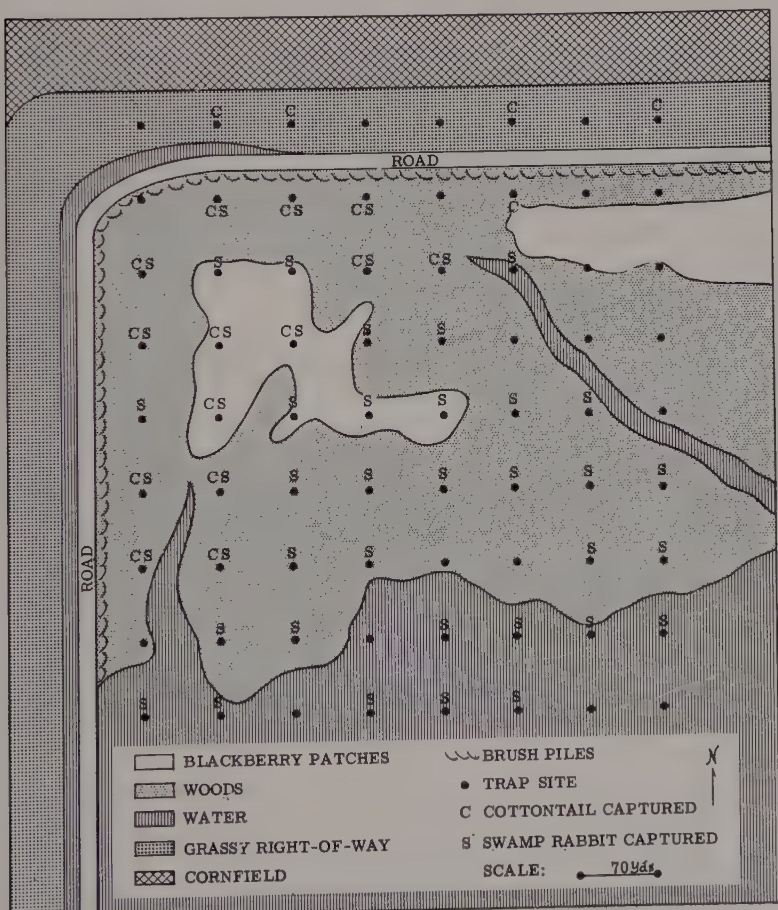

Fig. 1.—The trapping area.

num tag was placed in the ear of swamp rabbits (*S. aquaticus*), and a laminated plastic tag was attached to the other ear. The plastic tags were round or square, about one inch across, and were made of pieces of colored acetate plastic 0.015 to 0.020 inches thick. They were assembled in various color combinations and designs so that each rabbit could be identified individually. Plastic tags were attached to the ear by rabbit ear tags procured from National Band and Tag Company. None of the poultry tags was known to be lost, and the one plastic tag known to be lost came off when the rabbit was confined in a trap. With 7 × 50 binoculars, rabbits could be identified by the plastic tags as far away as 75 yards; since there were few openings of that length, the tags were generally satisfactory for the area.

Trapping results.—Traps were set for short periods starting in June, 1956; however, success was too low to warrant full-time trapping until November (Table I). Between November 15, 1956, and February 16, 1957, the traps were in constant operation.

During November most of the trap sites were on dry land. Water levels rose in December reaching a peak about the 18th. At that time the water boundaries were as shown on the map (Fig. 1), and although the traps were placed on logs or other dry situations, most traps in the southernmost two rows were surrounded by water. As the water encroached, trapping success diminished, and when water depth reached about six inches no more captures were made. During the period of trapping, 35 swamp rabbits were trapped a total of 143 times. Twenty-one of these rabbits were trapped at least three times each. The greatest number of captures for a single female was 16 and for a male, 8. Twenty-eight (80%) were captured more than once.

Eighteen cottontails were caught a total of 35 times. Recapture rates were much lower than those for the swamp rabbit. Only six of the cottontails were recaptured, and only one cottontail was caught more than three times. No attempt was made to estimate sizes of the home ranges of cottontails because of the low recapture rate,

TABLE I.—Monthly trapping success

Month	Trap nights	Captures of swamp rabbits	Captures of cottontails
June	60	0	0
July	224	3	0
August	336	0	0
September	432	2	0
October	0	....	....
November	720	40	11
December	1360	43	13
January	1800	39	10
February	1050	16	1

which may have indicated movement in and out of the trapping area.

Both Calhoun (1941) and Lowe (1958) indicated rather sharp delineation of swamp rabbit and cottontail ranges where both species occurred. In the present study, a gradation from cottontail to swamp rabbit ranges with a band of overlap, occurred within the trapping area (Fig. 1). Only cottontails were caught in the grassy right-of-way at the north end of the trapping plot. Both species were captured in a belt 70 to 140 yards wide bordering a road, and only swamp rabbits were caught deep in the wooded swamp. Cottontails were usually trapped farther from open water than were swamp rabbits but there were exceptions. In general, the cottontails were taken closer to the fields, road strips, and brush piles, but a considerable portion of the trapping area was tenable for both species.

Calculation of home ranges from trapping data.—Two systems for calculating areas in home ranges from trapping data were used. The first was to determine "minimum home ranges" as described by Mohr (1947): areas enclosed by lines connecting the outside points of capture for each rabbit were determined by planimeter. The second system involved the addition of "trap squares" as described by Haugen (1952). According to this system, which is one of several designed to add boundary strips, each trap within the grid is presumed to represent a square area extending halfway to the next trap; a home range is computed by adding "trap squares" in which the rabbit was trapped, plus any intervening squares.

Average home range sizes were computed only for swamp rabbits trapped four times or more; the choice of this figure was arbitrary. Results for these selected individuals are shown in Table II. Home ranges for seven females averaged 5.9 acres when computed by the "trap squares" method, and 2.1 acres when computed by Mohr's "minimum home range" procedure. Home ranges of seven males averaged 4.6 acres ("trap squares") and those of five males averaged 1.8 acres ("minimum home range"). Most investigators have found home ranges of male cottontails to be larger than those of females (Dalke, 1942; Bruna, 1952). In our study of swamp rabbits, results both of trapping and of beagle chases indicated that the females had the larger home ranges. Our data were gathered when there was little or no breeding.

Beagle chase procedure.—Most of the recorded chases of tagged rabbits by beagles were made in January and February. All recorded chases were made on the trapping area described previously. During most successful chases the observer was aided by one or two other persons.

When a chase was started one person stayed at the point of origin and tried to identify the rabbit by its ear tag when the rabbit returned. Many times the rabbit was identified when flushed and its identity checked upon its return.

Table II.—Home ranges of swamp rabbits trapped at least four times

Tag no.	No. of captures	No. of beagle chases	Sizes of home range in acres according to: "trap squares"	"minimum home range"	beagle chases	Maximum diameter of home range in yards derived from: trapping	beagle chases	both	Greatest departure of beagle chase from "minimum home range" (yards)
FEMALES									
409	16	3	8.0	4.0	4.6	210	234	242	84
414	13	3	9.0	3.5	3.5	284	280	350	79
450	11	2	7.0	2.5	5.5	219	263	263	84
418	9	2	6.0	2.0	3.4	219	238	252	46
460	6	2	4.0	1.0	2.5	219	284	284	89
406	6	--	4.0	1.0	----	140	------	------	----
430	5	3	3.0	1.0	5.0	156	298	298	130
Averages			5.9	2.1	4.1	208	266	282	85
MALES									
444	8	--	7.0	2.4	----	280	------	------	----
425	6	--	5.0	1.5	----	159	------	------	----
441	5	1	4.0	----	1.9	210	140	215	93
417	4	3	4.0	2.0	2.6	158	200	205	93
413	4	1	6.0	2.0	1.7	280	130	280	24
442	4	2	4.0	1.0	1.6	196	163	233	82
415	4	--	2.0	----	----	98	------	------	----
Averages			4.6	1.8	2.0	197	158	233	73

One person followed closely behind the dogs, and marked the trail with tissue paper. Routes were retraced and recorded when the chase was over. The paper was picked up to avoid confusion on

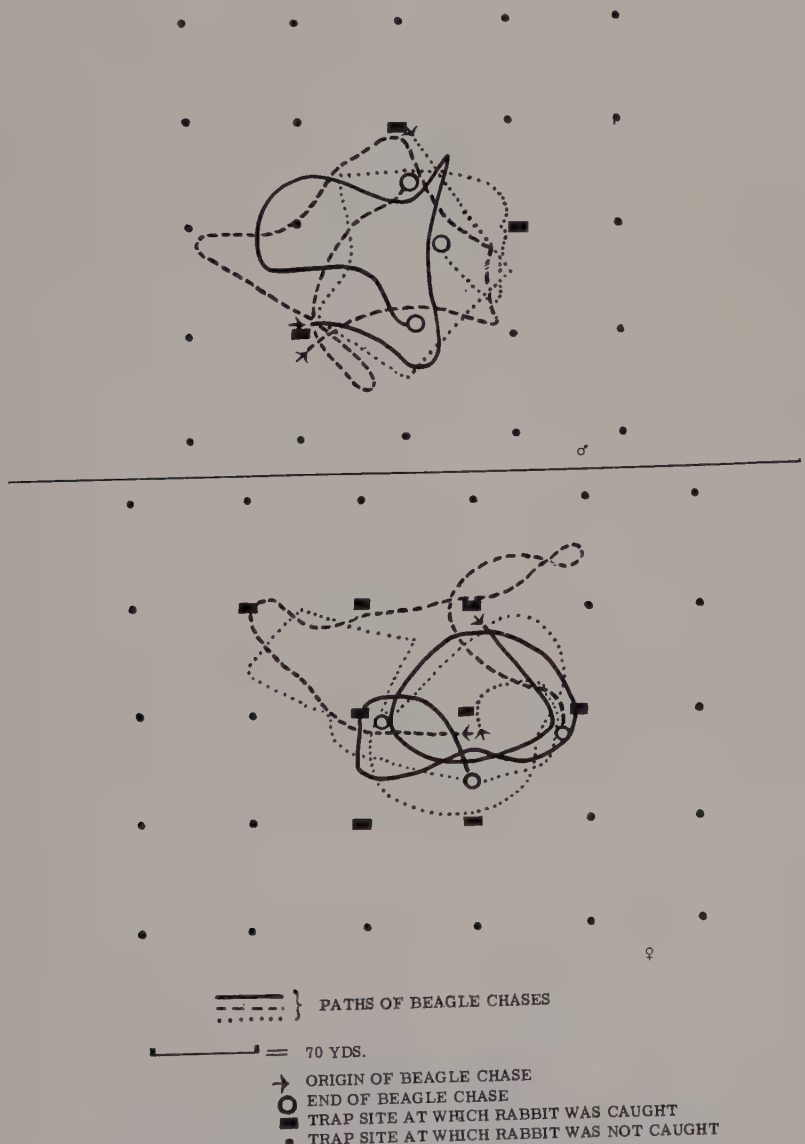

Fig. 2.—Trapping sites and paths of beagle chases for a male and a female swamp rabbit.

subsequent runs. Beagle chases were not recorded if the identity of the rabbit was uncertain, or if the dogs lost the trail for an extended period and the rabbit's identity could not then be rechecked.

Results of beagle chases.—A total of 29 chases of 15 individuals was made. Of these 15 rabbits, nine were females and six were males. The greatest number of acceptable chases of any individual was three. The route taken by the rabbit was plotted to scale and the area calculated with a planimeter. The maximum home range determined by this method was 5.5 acres for a female and 7.9 acres for a male. These ranges are much smaller than those reported by Lowe (1958) for swamp rabbits in Georgia; the latter averaged about 19 acres.

The similarity in the routes taken by the same animals on separate runs is apparent in Figures 2, 3, and 4. These figures also show

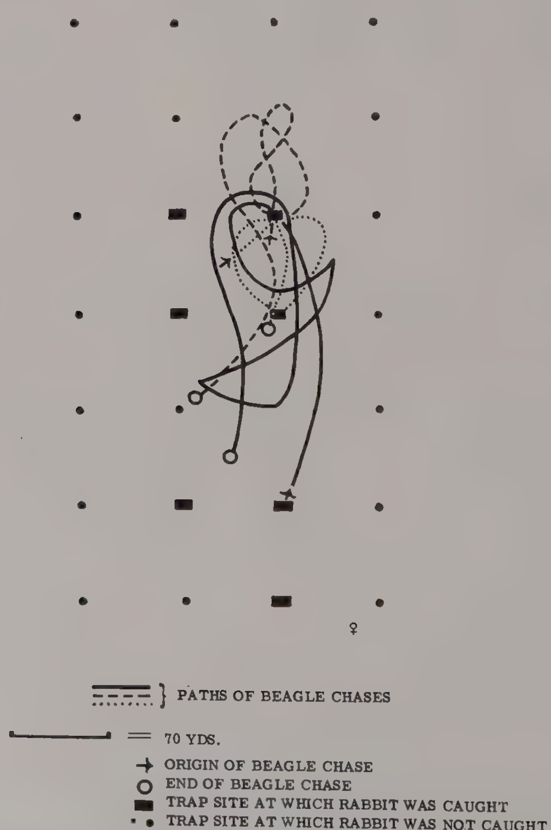

Fig. 3.—Trapping sites and paths of beagle chases for a female swamp rabbit.

the close correspondence between successful trap sites and the routes taken during beagle chases. Another expression of this correspondence is the fact that the greatest departure of a beagle chase from the "minimum home range" for a rabbit trapped four or more times was 130 yards. This information, as well as a summary of home range

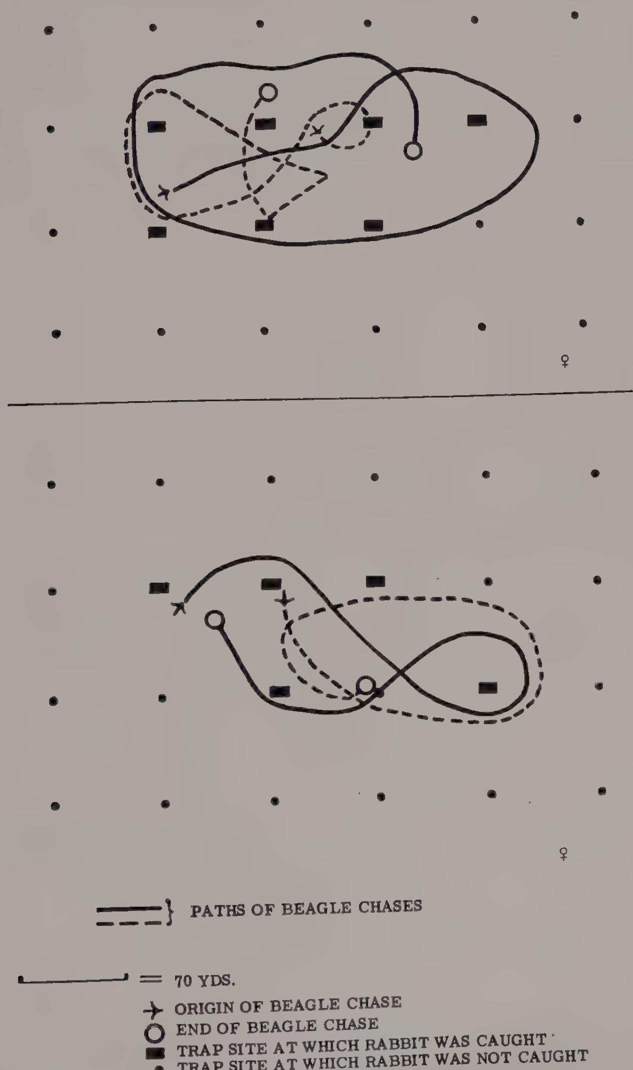

Fig. 4.—Trapping sites and paths of beagle chases for two female swamp rabbits.

sizes as determined by several methods for rabbits trapped four or more times is shown in Table II. Included in the table are measures of "maximum diameters" or the greatest distance between any points in an indicated home range.

Overlapping ranges.—The great extent of overlapping of home ranges is illustrated in Figure 5 where home ranges of 11 males, determined by trapping and beagle chases, are plotted in spatial relationship. Home ranges of the females overlapped similarly, and those of males and females overlapped one another. Lowe (1958) thought that home ranges of the swamp rabbits in Georgia overlapped but little. The density of his swamp rabbit population was much lower than ours (about one rabbit per 18 acres on his area *vs* one per 1.5 acres on ours), and this fact may help explain the greater overlapping and smaller home ranges we found.

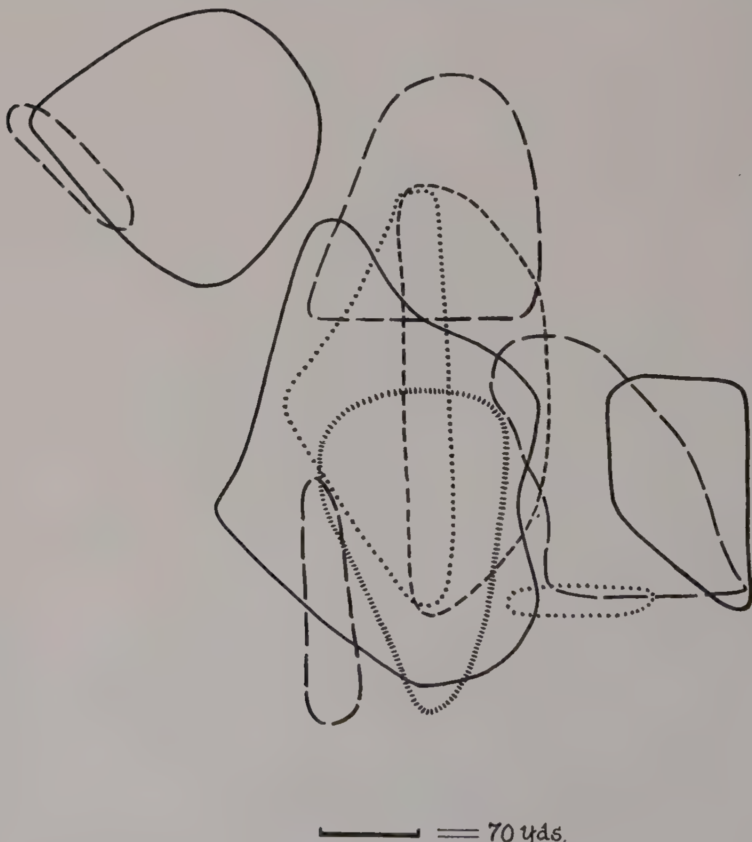

Fig. 5.—Overlapping home ranges of 11 male swamp rabbits.

Beagle chases as a means of determining home ranges.—Chasing by dogs has been used to give some information about sizes of home ranges of the marsh rabbit (*Sylvilagus palustris*) by Carr (1939) and for the swamp rabbit by Lowe (1958). However, neither of these workers gathered detailed information about individually-marked rabbits by chasing with dogs, and the data they secured were not related to trapping records.

The adequacy of beagle chases in determining size of home ranges is worthy of discussion. One might wonder how often in the course of a chase the beagle shifted to a different rabbit. In our study this could have happened rarely, if at all, because: (1) during several chases rabbits were individually identified more than once, and (2) whenever there was real doubt about this point, the record of the chase was discarded.

A second question is whether paths of beagle chases really represent home ranges, even when accurately mapped. This question cannot be answered categorically, but the fact that the rabbits usually return to the point of origin of the chase implies that they tend to remain within a familiar area. Howard M. Wight (Pers. Comm.) has observed cottontails that were released several miles from their home ranges running in a straight line when chased by a dog. Thus a rabbit pushed out of its home range might run in a straight line and the pattern of the chase would be quite different from those shown in Figures 2-4. Further, beagles of the type we used are often far behind the rabbit. During a chase, rabbits were sometimes seen to stop and lick themselves in leisurely fashion. It is hard to imagine that under such circumstances the animal is being pushed out of its home range. Additional evidence that beagle chases accurately estimate home ranges is provided by the correspondence between the successful trapping sites and the area enclosed by beagle chases, as well as the similarity of areas enclosed by different chases of the same rabbit.

In evaluating the "trap squares" method and the "minimum home range," Hayne (1949) noted that the critics of the "trap squares" approach believe that it gives an estimate that is too large, and critics of the "minimum home range" think that it gives an estimate that is too small (Hayne, 1949; Stickel, 1954). Interestingly, in six of nine cases, the estimated size of home range obtained by beagle chases fell between the sizes obtained using the other two methods.

One advantage of determining home ranges by beagle chases is the rapidity of the method; another is the simplicity of determining and expressing results.

REPRODUCTIVE HISTORY

Onset of breeding season.—The start of the reproductive season in cottontails is controlled by the breeding condition of the female, for as Hamilton (1940) pointed out, the male is capable of breeding

before the female and remains fertile after the female is no longer in breeding condition. In Texas, Hunt (1959) found that some individuals of both sexes of swamp rabbits were in breeding condition throughout the year, but reproductive activity diminished in the fall.

In Missouri it appears that a definite anestrous period may occur since no adult female collected between November and the end of January was reproductively active. A pre-estrous female was taken February 25, 1957, and two more pre-estrous animals were taken March 9, 1957. On March 16, 1957, a recently post-partum female in full lactation was collected. Back-dating 40 days (an average of Hunt's estimated gestation period, for the swamp rabbit), February 4 was estimated as the conception date. Similarly five more females were estimated to have been bred during February. Collections were not sufficient to determine the month when breeding activity terminated, but this apparently occurs by late summer.

Breeding condition in males.—Testes were preserved from some males during each month, October, 1956, through June, 1957. Histological sections were prepared from one testis and cauda epididymis of each male. If sperm was found in the testis and the tail of the epididymis, the rabbit was considered to be in breeding condition. Material from 42 animals was analyzed.

Since no collections were made during August and September, the reproductive status through this period is unknown. In October four males were collected and only one of these was in breeding condition. During November three adult males were collected. One of these had no sperm in either the testis or epididymis while the other two showed active spermatogenesis. Three of the five males taken during December were producing sperm while two (one adult and one young) had no stages later than secondary spermatocytes in the testes. All animals taken throughout spring and early summer were reproductively active.

Some male swamp rabbits in Missouri populations may be in breeding condition every month of the year. Because no collections were made in the late summer this statement cannot be supported with direct evidence. Probably the number of breeding males begins to decline during the late summer and remains low through November. By the end of December both juvenile and adult males are in breeding condition.

The testes of reproductively active swamp rabbits are conspicuously smaller than those of breeding cottontails as Layne (1958) has noted. The average weight of both testes from 10 Missouri cottontails taken in March was 21.5 grams while the average weight for both testes from 10 swamp rabbits taken in March was 3.9 grams.

Litter size.—Litter size was estimated by three methods. The first was to count the corpora lutea of all swamp rabbits collected between March 16 and June 23, 1957. Forty-six females had an average corpora lutea count of 3.7 (range 2-6). These figures indicate maxi-

mum litter size and would not account for post- or pre-implantation losses.

The second approach was to count the embryos found in the pregnant females. Only embryos having a crown-rump measurement of 35 mm or more were included. Excluding embryos of small size lessens the error introduced by resorptions occurring in later pregnancy. Embryos in 14 females were counted; half of them had 3 embryos and the average was 2.8 (range 1 to 4). When 24 females with embryos of all sizes were included, the average litter size was 3. Hunt's (1959) embryo counts averaged 2.8 (range 1 to 5) for 29 female swamp rabbits. Svihla's (1929) embryo counts averaged 3.7 (range 3 to 5).

The last approach was counting placental scars. Those counted were probably not more than two weeks post-partum. The average placental scar count in 7 rabbits was 3.4 (range 3 to 4). Conaway (1955) showed that in rats the placental scars formed at the sites of resorbed embryos were indistinguishable from those formed at the sites of term embryos. If this is also true in the swamp rabbit, the placental scar method would result in an overestimation of litter size.

FOOD HABITS

The plant most commonly eaten by swamp rabbits was *Carex lupulina,* locally called swamp grass. This plant is abundant throughout the study area and is used by swamp rabbits from spring until mid-winter. During the same period large amounts of hazelnut (*Corylus sp.*) shoots were eaten. After the *Carex* died-back in late December or early January, swamp rabbits began eating twigs and bark of woody plants. The four most-used plants during the late winter months were blackberry (*Rubus spp.*), hazelnut, deciduous holly (*Ilex decidua*), and spice bush (*Lindera benzoin*).

Table III lists plants used, time of usage, and a coarse measure of abundance of plants. Care was taken to record plants only in the area used by the swamp rabbits and not used by cottontails.

During a two-month period of flooding in spring, 1957, swamp rabbits were forced on to roadways running through the Mingo Refuge. They ate Alta fescue, winter wheat, and sericea lespedeza (*L. cuneata*).

In other areas, swamp rabbits are reported to eat a wide variety of grasses, sedges, forbs, and barks and shoots of trees (Svihla, 1929; Smith, 1940; Calhoun, 1941).

Coprophagy.—Soft pellets occurred frequently in the stomachs of the swamp rabbits and cottontails that were collected. During the later part of the study all rabbits collected were examined for soft feces in the stomach and rectum. Information obtained was recorded in hourly intervals (Fig. 6). These small samples indicate that coprophagy occurs mainly during the daylight hours when the rabbits are resting, and not at night, when they are feeding. This is the pat-

TABLE III.—Plants used as food by swamp rabbits

Species	Amount of usage	Season used	Abundance of plant
Sedge (*Carex lupulina*)	heavy	spring summer, fall & early winter	very common
Blackberry (*Rubus* spp.)	heavy	fall & winter	very common
Hazelnut (*Corylus* sp.)	heavy	fall & winter	very common
Deciduous holly (*Ilex decidua*)	heavy	winter	common
Spice bush (*Lindera benzoin*)	heavy	winter	common
Hackberry (*Celtis laevigata*)	medium	winter	common
Sumac (*Rhus aromatica*)	medium	winter	common
Sassafras (*Sassafras albidum*)	medium	winter	rare
Trumpet vine (*Campsis radicans*)	light	winter	very common
Hercules club (*Aralia spinosa*)	light	winter	common
Overcup oak (*Quercus lyrata*)	light	winter	common
Pin oak (*Quercus palustris*)	light	winter	very common
Elm (*Ulmus americana*)	light	winter	common
Elm (*Ulmus rubra*)	light	winter	common
Cherry bark oak (*Quercus falcata* var. *pagodaefolia*)	light	winter	common
Hickory (*Carya* spp.)	light	winter	common
Green brier (*Smilax* spp.)	light	winter	common
Paw paw (*Asimina triloba*)	light	winter	rare

tern observed in the jack rabbit by Lechleitner (1957). Layne (1958) has also reported coprophagy in the swamp rabbit.

SUMMARY

1. Thirty-five swamp rabbits were trapped 143 times on a 72-acre area. Traps were located in a grid pattern, 70 yards apart. All rabbits were tagged with colored plastic tags which made field identification of individuals possible.

2. Home ranges for females trapped four times or more averaged 5.9 acres when computed by addition of "trap squares," and 2.1 acres when determined by the "minimum home range" method. Corresponding figures for males were 4.6 and 1.8 acres.

3. Sizes of home ranges were also estimated by chasing individually tagged rabbits with beagles, and recording the paths of the chases. Home ranges determined in this fashion averaged 4.1 acres for females and 2.0 acres for males. Routes taken by rabbits during beagle chases correspond very closely with trapping records for the same individuals, and with routes taken by the same rabbits in different chases. Beagle chases appear to have much promise for determining home ranges of rabbits. Data can be gathered rapidly and

interpretation is simple. Evidence for the validity of this method is (1) that in six of nine cases the estimated size of home range obtained by beagle chases fell between the home range sizes estimated by "trap squares" and "minimum home ranges; (2) that successive chases of the same animal encompassed similar areas.

4. Female swamp rabbits in southeast Missouri were probably in estrus by early February, and only one female was found reproductively inactive after February 25. No females collected from October through January were in breeding condition. Males attain breeding condition before the females and remain in it longer. Some male swamp rabbits probably are capable of breeding throughout the year.

5. Litter sizes were estimated from corpora lutea counts, embryo counts, and placental scar counts. From corpora lutea counts, the average was 3.7 (range 2 to 6). From embryo counts, the average was 2.8 (range 1 to 4). From placental scar counts the average was 3.4 (range 3 to 4).

6. The plant most commonly eaten by the swamp rabbit was *Carex lupulina*. This plant was eaten until late winter, when it was no longer green. The four most-used plants during the late winter months were blackberry, hazelnut, deciduous holly, and spice bush.

7. Coprophagy was found to be practiced regularly by both swamp rabbits and cottontails. Coprophagy seemed to occur in the daytime during the resting period, and was discontinued at night during feeding.

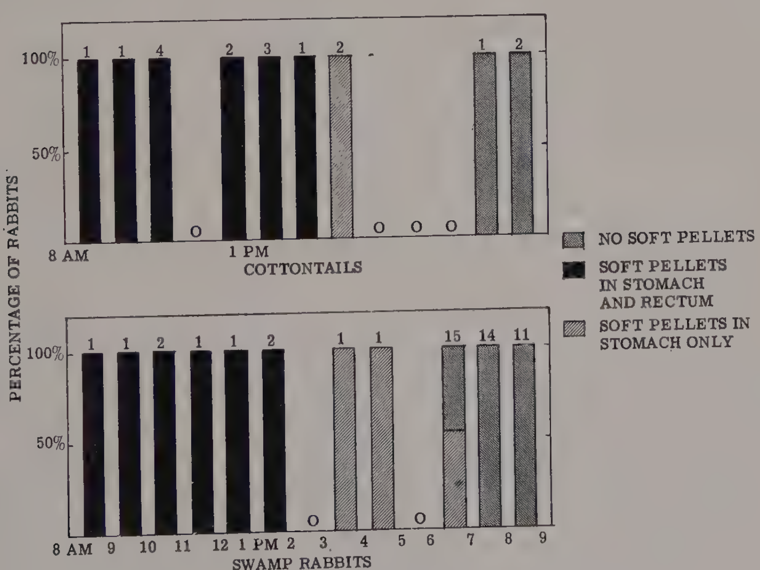

Fig. 6.—Percentages of cottontails and swamp rabbits containing soft pellets.

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Notes on the Following Response and Other Behavior of Young Gray Squirrels

JACK P. HAILMAN[1]

In spite of the fact that a prodigious number of papers on the gray squirrel, *Sciurus carolinensis*, have been published (see bibliography of Flyger, 1951), little is known about the behavior of the young after leaving the nest. This paper presents some preliminary observations on young gray squirrels during the post-nest period, and describes for the first time the "following response" of this species.

Observations

On May 23, 1958, on the grounds of Harvard University, Cambridge, Massachusetts, I saw two squirrels foraging together on the ground; the seemingly peculiar behavior of one drew my attention. This individual approached the other and nuzzled its flanks and shoulder region at intervals of 10-20 seconds. It soon became apparent that this was a young squirrel, as evidenced by its slightly browner coat, smaller body, and relatively larger head, and by the fact that it was following an adult, presumably its mother. This nuzzling behavior continued as they moved across the grass, the young coming to the adult whenever they passed. When the two approached to within six feet of a tree, the young animal broke company and ran to the tree, leaping about a foot up its side in the usual *Sciurus* manner. Here it paused, clinging, and looked toward the adult, which made no detectable noises or movements. The young squirrel then bounded back to the adult and again began vigorously sniffing the shoulder area of the parent. A passing automobile frightened both individuals and the observations were terminated.

The second incident took place on June 2nd in a different part of the Harvard campus. An adult, followed by three young, descended a tree head-first. The young executed the same sniffing motions observed above. Each time the female stopped, the young squirrels moved in and sniffed her back and sides, pushing each other aside. This behavior continued when they reached the ground, and throughout the observations described below. No "play," as such, was observed in the animals, although they often scrambled over one another on the ground in order to keep close to the female. The adult hopped to a nearby fence, which she climbed easily. The first young squirrel to follow was clumsy, but successful, and immediately went to the adult and sniffed her sides. The second young animal to attempt the ascent fell twice from the half-way point, and gave up. The third individual, continually watching the adult, did not try to climb the fence. About a minute later,

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the adult and the first young animal rejoined the other two on the ground; the group began foraging across the grass together, with the three young squirrels intermittantly sniffing the female.

One young squirrel became separated from the rest, and began picking up and manipulating items in the grass, including a small stone. The animal was frightened by another person, and leapt onto a nearby basement window pane from which it fell. Later, the squirrel climbed a tree, and observations ceased.

Several groups of gray squirrels were observed on April 25, 1959, in the Municipal Gardens at Norfolk, Virginia. The first group consisted of two young and an adult. Upon my approach, they congregated in the same tree and began to climb upward. As my wife and I arrived at the base of this tree, the young squirrels began to move through the tree tops in separate directions. For a moment or two the adult chattered at me, but then ceased and also began moving away through the trees. I followed one of the young squirrels to study how it climbed and jumped. The woods in this area consisted of various deciduous species, chiefly oaks, and the squirrel climbed to a height of roughly forty feet. The animal was quite agile at climbing and moving along limbs, but was inexperienced in executing leaps from one tree to another. It often hesitated before jumping, and twice, after pausing, it did not jump, but ran back toward the trunk and then out another limb.

Twice again that day we saw groups of squirrels, once with three young, the other time with four, but no adults were with these groups. Although no detailed notes were taken on these latter groups, all the young of these groups appeared to be quite agile at climbing and leaping.

Discussion

DEPENDENCY PERIOD

The time during which the young follow and forage with the mother I have designated as the "dependency period," to correspond with the terminology used for the analogous period in birds (Brackbill, 1953). Tentatively, this period is defined for squirrels as extending from the time when the young leave the nest initially until they are no longer dependent upon the mother (or any adult squirrel) for food or protection. The dependency period is probably a time of transition during which the young squirrel adjusts to life outside the nest. Since bands of young may be seen in the fall and winter (Shorten, 1954: 116-117; Flyger, 1955), it is probable that family ties are not completely severed until the first spring of life, at least in some cases, although the amount of dependency, if any, upon the parent during this time is unknown. The fact that the male may sometimes take over the raising of the first litter when the female becomes pregnant with the second (Shorten, 1954) also complicates the delineation of the dependency period. However, the original definition offered above is adequate for purposes of this paper, and may later be refined.

Standard life history references (e.g., Seton, 1928; Hamilton, 1943; and Burt, 1943, 1957) all omit any description of behavior during the dependency period of the gray squirrel. Shorten (1954:137-138) merely mentions that upon leaving the nest, young follow the mother. I discuss below some new questions and problems raised by my observations on young squirrels, and comment on the development of certain behavior patterns during the dependency period.

FOLLOWING RESPONSE AND IMPRINTING

Many young animals are known to follow their parents upon leaving the nest (Thorpe, 1956:397), but there are few careful descriptions of the "following response" in mammalian species. The observations above indicate that the young gray squirrels rely heavily on olfactory clues of the parent, as evidenced by their continual sniffing. A cursory search of the literature indicates that the badger (*Meles meles*) is the only animal in which the young are known to sniff frequently during following (Neal, 1958:35). Young birds react primarily to visual and auditory stimuli while following (Thorpe, 1956:116, 357ff).

It seems quite likely that an olfactory basis for the recognition of the mother is advantageous to young squirrels inside the nest for several reasons: (1) the eyes do not open until the 36th day (Burt, 1957: 102); (2) even after the eyes are open, darkness hinders formation of visual recognition, especially in nest-holes. We know that adult squirrels maintain a dominance hierarchy where each individual recognizes all others at distances which seem to preclude good olfactory discrimination (Flyger, 1955). Furthermore, the species' social communicative behavior (or "ritualized" signal behavior) seems to depend largely on visual and auditory signs (Flyger, *ibid.*). It is known also that the gray squirrel is quite dependent upon its visual sense in general behavior (Yoakum, 1902), and that this species has a poorly developed olfactory sense compared to other sciurids (McClelland, 1948), at least as adults. Therefore, the problem of transition from nest life olfactory recognition to adult visual (and auditory) recognition seems to be an important one in the animal's life.

During the following response both olfactory and visual stimuli seem to be important in the parent-young bond, and this may well be the period of transition from one to the other. It is possible that a very rapid emphatic learning, such as "imprinting," occurs at this time, or, on the other hand, that the transition is a gradual one. Imprinting is the term applied to the rapid process by which young birds (and other animals) learn the recognition characters of their species while following the parent (Thorpe, 1956:115-117, 357-367). Imprinting has been reported for many mammals (Thorpe, 1956:397), and probably even exists to some extent in humans (Bowlby, 1953). That young squirrels may become imprinted with the visual recognition characters of their parents during the following behavior seems possible.

It is tempting to think of the olfactory to visual ontogenetic changes

as recapitulating the phylogeny of nocturnal ground dwelling animals dependent primarily upon smell as chief sensory input to the diurnal, arboreal gray squirrel dependent on its visual acuity as the basis of behavior. Perhaps this oversimplifies the problem, but there seem to be selective advantages in retaining olfaction: (1) its use in the nest, as discussed above; (2) its possible advantage in the following response, discussed below under "locomotion and foraging."

Experience during the following period is also thought to affect later sexual behavior of the individual (Thorpe, 1956), although the exact relationship involved is not yet clear. Flyger (1955) notes that the sexual behavior of the gray squirrel is strongly dependent upon certain olfactory clues, and there could exist a connection between this and early olfactory experience.

LOCOMOTION AND FORAGING

The actual motions of climbing, running, jumping, etc., seemed well-developed in all young gray squirrels. Young will cling to, and apparently climb, a tree before their eyes are opened (Smith, 1947); this seems to indicate that these motions develop largely independent from any individual experience. Apparently the young squirrel learns during the dependency period how to use its motor patterns; it learns: (a) which vertical surfaces are climbable; (b) how to choose limbs to jump from one tree to another; and (c) how to choose footholds in climbing difficult objects, such as a board fence. The partial dependence upon olfactory stimuli while following the mother necessitates that the young squirrels stay close to the mother. This, in turn, not only provides better protection to the young but also may encourage them to develop locomotor agility by following the parent in difficult movements. These selective advantages may contribute to retention of olfactory sense during the dependency period (see above).

Just as the young squirrel must learn what is "climbable," so it must learn what is "edible," and foraging during the dependency period may provide that experience. Besides the selection of food, other feeding behavior, such as the opening of nuts, improves during this time (Shorten, 1954).

SUMMARY

Preliminary observations made during the spring of 1958 and that of 1959 on young gray squirrels (*Sciurus carolinensis*) point out new facts concerning the post-nest life dependency period. While following (probably the mother), young squirrels constantly nuzzle the adult's flanks, and probably are dependent upon both visual and olfactory stimuli to motivate the "following response." Selective advantages of retaining the olfactory sense as primary during this period are discussed, and the possibility of a rapid, emphatic learning of visual species recognition characters during the following response is suggested. The motor patterns of locomotion are well-developed and young probably

gain experience on how to use these while following. Foraging may also improve during the dependency period.

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On Another Biclitellate Earthworm[1]

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The biclitellate condition has been recorded hitherto from five individuals (Gates, 1956b), including four *Lumbricus terrestris* L. and one *Eisenia foetida* (Savigny, 1826). The latter (Gates, 1956a, 1958) is relictus-like on one side of the body. The term "relictus-like" refers to the position of the reproductive apertures, well behind normal locations. Two specimens have been described in the literature on earthworms. The type of *relictus,* subsequently shown (Gates, 1956a) to be an aberrant specimen of *Lumbricus rubellus* Hoffmeister 1843, has male pores on segment xxviii. The relictus-like specimen from Arizona, originally referred to *Allolobophora caliginosa* (now known to be a complex of several morphologically distinguishable forms) but which can now be identified as *A. trapezoides* (Duges, 1828), has male pores on xxviii-xxix.

An additional biclitellate specimen of *E. foetida* that is relictus-like on both sides was found in a small sample (25 worms) from culture beds of an earthworm farm at Laconia, N. H. The aberrant worm became available through the courtesy of Mr. Oscar Morrisette.

Description

First functional dorsal pore at intersegmental furrow 5/6, a smaller pore-like marking at 4/5. Reproductive apertures at usual locations with reference to meridians of longitude such as B, mD, etc. Clitellum at maximal tumescence. Tubercula pubertatis unrecognizable. Calciferous gland extends, at least, through segments xviii-xxi. Gizzard in xxviii-xxix. Ventral blood vessel bifurcates in v, each branch passing anterolaterally beyond circumpharyngeal nerve commissures. Dorsal trunk unrecognizable anterior to 9/10 (invisible because of lack of blood?). Brain, anteriorly in iii. Balls of brown debris, such as may be found after breeding has ceased, are present in some seminal vesicles. Spermathecal ampullae are filled with a watery fluid.

Metamerism, along much of the main axis, is abnormal beginning with xiii which is involved in a spiral. Segment xix of left side ends mesially both dorsally and ventrally. Among abnormalities partly concealed by clitellar obliteration of intersegmental furrows are two compound metameres each of which seemingly is split into three segments on the opposite side. Helicometameres are frequent behind the clitellar region, the last terminating with the eighth segment from the hind end. Further specification as to the metameric anomalies is need-

[1] From research financed by the Rockefeller Foundation.

less, but their existence requires that the rest of the anatomy be characterized as to left or right sides of the body.

Left side. Segments, 164. Spermathecal pores at 15/16, 16/17, 17/18 and 20/21. Female pores, in xxi and xxv. Male tumescence, with normal cleft (male pore unrecognizable), in xxv. Clitellum on xlv-liii, lvii-lxi and lxv-lxvi.

Intestinal origin in region of xxv-xxvi. Typhlosole ends in 151st segment. Hearts in x-xviii and xxi. Testes and male funnels (unusually large), in xvi, xvii, xviii, xxi. Seminal vesicles, preseptal in xv, xvi and xvii, postseptal in xviii and xxii. Ovary, with mature ova (some in egg string) and female funnel in xx. Ovary (no egg string or mature ova) and normal female funnel in xxiv. Ovisac in xxi but none in xxv. Spermathecae in xv, xvi, xvii and xx. Male gonoducts, as on other side of body, could not be traced (ventral parietes extensively blistered).

Right side. Segments, 160. Spermathecal pores at 15/16, 16/17, 17/18. Female pores, in xxi and xxiii. Male tumescences, each with a cleft (but male pores unrecognizable), on xxv and xxvi. Clitellum on xliii-li and lv-lxiv.

Intestinal origin in xxvii. Typhlosole ends in 149th segment. Hearts in xi-xviii. Testes and unusually large male funnels in xvi, xvii, xviii. Male funnels of xvii and xviii, like those in xvii-xviii on left side, with brilliant spermatozoal iridescence. Other male funnels with no trace of the iridescence. Seminal vesicles, preseptal in xv and xvi, postseptal in xvii, xviii, xix. Ovary (no egg string or mature ova) and normal female funnel in xx. Ovary with mature ova (some in egg string) and female funnel in xxii. Ovisac present in xxiii but lacking in xxi. Spermathecae, preseptal as on left side, in xv, xvi, xvii.

Discussion

Segment number in unamputated normal individuals of *E. foetida* in North America, according to the author's unpublished counts, is 90-120. There are, then, in the specimen now under consideration forty to seventy or even more extra metameres. They were not added on at the hind end of the body, the atyphlosolate portion of the intestine which extends through 11-13 segments (11-15 in normal specimens, Gates, unpublished manuscript) being of usual length. As the extra metameres were not produced in the normal annelid manner (by a growth zone in the anal region) they must have been inserted in some unusual way. Situation of the gonads (which have a uniform location in all normal earthworms) shows that some segments were inserted close to the front end, others further back and also differently on each side. Intercalations such as are presently required do not take place in any species of earthworm, so far as is known, after hatching. Their origin then must be sought during embryogenesis and presumbly after formation of the germ layer in which metameric segmentation first appears. Associated with that modification of mesoblast

development is an increase in number of fixed position organs such as testes and ovaries. Most of the divergence in location and number of those structures in previous specimens could be explained (Gates, 1956-1958) by halving of mesoblastic somites at appropriate levels provided each daughter portion retained full developmental capacity of the parent block. What then are the levels at which somite splitting, with retention of original potentiality, could provide the aberrations of the present specimen.

Hearts are present in normal individuals, according to previous records (Gates, 1956, p. 21) and subsequently secured data, only in vii-xi. Location of the first heart of the left side in x shows that three segments were intercalated anteriorly. The three somites that were halved are assumed, in absence of information permitting precise specification, to be those at the 4th to the 6th level, *i.e.*, those that otherwise would have become segments iv-vi. Presence of ten instead of five hearts requires each of the heart-producing somites at the 7th to the 11th levels to have been halved. The number of testes, seminal vesicles and spermathecae corroborates splitting of somites at the 10th and 11th levels. The two ovary-containing segments indicate that the somite at the 13th level also was halved. Since the male tumescences are in xxv instead of xv there must have been ten intercalations in front of the 15th level. Nine already have been accounted for. The other intercalation could have resulted from halving of a somite at the 12th or 14th level neither of which give rise to organs of fixed position. Location of the gizzard (normally in xvii) seems to require halving of a somite at the 15th or 16th level. The latter is the one involved as halving of the former would have given two segments with male tumescences as in the relictus-like worm from Arizona (Gates, 1956, p. 369).

The clitellum of normal American individuals of *E. foetida* that have been seen by the writer comprises 6-8 segments (see below). Clitellar extension through 16 segments of the present specimen suggests halving of eight somites which could have been at the 24th-31st, 25th-32d or 26th-33d levels. As the clitellum begins with the 45th segment, there are 21-11=10 or 20-11=9 yet to be accounted for if the first clitellar somite were originally at the 24th or 25th level. But splitting of each somite at the 17th-23d or 24th level will not provide the necessary intercalations. If the first clitellar somite were at the 26th level, only 19-11=8 insertions are required. Splitting of all but one of the somites at the 17th-25th levels permits the clitellum to begin with the 45th segment. The remainder of the 13-43 possible intercalations on the left side would then be between the 33d level and the last 13 segments. Absence of special organs obviates localization of insertions in that region. Unexplained by the somite halving is the separation of a normally continuous clitellum into three parts and more particularly presence of three non-clitellar somites between 29a and 29b (presumably) as well as between 31b and 32a.[2]

[2] Daughter somites are indicated by a and b after level of the parent block.

On the right side, location of the first heart shows four segments were intercalated anterior to vii. Though they could have arisen from splitting of somites at any four of the 2d[3] to the 6th levels, fragmentation is assumed to have been at the 3d to the 6th levels. Eight hearts require halving of only three of the somites at the 7th-11th levels. The testes show but one of the somites at the 10th-11th levels were halved, hence the others must have been two of those at the 7th-9th levels. Two ovary-containing segments require halving of the somite at the 13th level. Two male tumescences require halving of the somite at the 15th level. Location of the male tumescences in xxv-xxvi requires ten insertions in front of the 15th level. Only eight have been provided. The additional two intercalations must have been between the 11th and the 15th levels. Hence, somites at the 12th and 14th levels obviously were the ones involved. If the first clitellar somite was that at the 26th level as on the left side, any six of the ten somites at the 16th-25th levels could have been halved. Then, to produce the 19-segment clitellum of the right side, 9 of the somites at the 26th to the 35th level must have been halved while one was not. But the clitellum has not been found to extend, in normal specimens of *E. foetida,* into xxxv though limits often are difficult to determine precisely from external inspection. If the first clitellar somite of the right side was at the 25th level, 7 of the somites at the 16th-24th levels must have been halved. The 19-segment clitellum then would have been derived from splitting of all but one of the somites at the 25th to the 34th level. This appears to be less improbable as there is one record (Gates, 1943, p. 95) of a clitellum extending through xxxiv.[4] Somite halving on the right side does not explain separation of the clitellum by three non-clitellar segments into two discrete portions nor the presence of an agonadal metamere between the two that contain ovaries.

Inasmuch as development is determinate and gonads are organs of fixed position, the aberrant locations of testes and ovaries in the present specimen should have resulted not from organ shifts (*i.e.,* transfer of potentiality) but rather from somite translocations. The abnormality of so much of the external metamerism in the present specimen shows there had been, as it were, considerable interference to normal median union. Such "interference" must be common in lumbricid development judging from the anomalies of adult metamerism that are found so often. Those aberrations arise through union

[3] The most anterior split required in any of the author's specimens has been at the 2d level, *i.e.,* of the somite that becomes segment ii. The mesoderm of a more anterior portion of the embryo that becomes the peristomium (segment i) then may not be so organized as to be liable to fragmentation.

[4] The clitellum of *E. foetida,* according to Michaelsen (1900, p. 476 and repeated by Stephenson, 1923, p. 499, Cernosvitov & Evans, 1947, p. 22), covers 7-9 segments, 24, 25, 26-32. It covers, in North America according to the author's records, 6 segments (5 specimens), 7 segments (72 specimens), 8 segments (9 specimens), and is on 25, 26, 27-31, 32, 33, 34.

of a somite of one side with two or even three on the other side, union dorsally with one somite but ventrally with another somite of the opposite side, sometimes isolating a somite from any union.

The serial order of ovarian segments on the right side then could have resulted merely by a daughter half-somite from the 12th or from the 14th level being forced out of normal position and then in between 13a and 13b. On the left side more complicated rearrangements that seem to be required could have been made in several ways. Possibly daughter somite 11b was forced out of position, back of 12 and then into line again behind 13a while 13b was being pushed in between 14b and the undivided somite at the 15th level.

In the clitellar region, on each side of the body, somites presumably from the postclitellar region, were forced forward into positions so as to separate the clitellum into three and two portions, respectively, on left and right sides.

Halving of mesoblastic somites early in development of the aberrant worm explains adequately the number of segments and of fixed-position organs as well as much of the homoeosis. Situations of several organs that are not in normal serial order require *in toto* translocation of somites before and/or after halving. The mesoblast may then be divided during development into discrete somites that can be forced out of normal position and into quite unusual locations. If, however, the mesoblast is not physically separated into discrete units, it appears to be capable of being transected along potential somite boundaries. Fragments so produced can be rearranged without loss of developmental potentiality determined by the original axial positions.

Presence of an ovisac in a testis segment (as in Lxxi) raises no difficulties as its development there is believed to be induced by the ovary of 13a which became segment xx. Presence of a spermatheca in an ovarian segment (Lxx) also raises no questions even though the receptacles always are one or more segments in front of the female gonads in normal individuals. Development of the spermatheca obviously was controlled by the testis somite that became Lxxi. Presence of seminal vesicles in segments where they normally would not develop is due to induction from the male gonads.

Unilateral translocations of somites only are suggested above. If, however, somites can be forced from one side of the embryo to the other, various displacements of that sort could have produced the conditions exemplified by the present worm. Abortion and trisection (*cf.* compound metameres mentioned on p. 418) of somites were mentioned in previous communications as ways of providing unexplained residues of homoeosis in some of the previous specimens. Somite translocation was considered at the time but was not mentioned because of lack of evidence from fixed-position organs such as testes and ovaries. That evidence now has been found and in further aberrant specimens indications of translocation from one side to the other are awaited.

SUMMARY

Number of segments and of fixed-position organs in a biclitellate and relictus-like specimen of *E. foetida* are explained by somite halving, providing developmental potentiality of the parent block is retained. Out-of-order location of certain organs requires translocation into abnormal positions of embryonic somites. The translocations indicate that somites are discrete or that a continuous mesoblast can be transected at potential boundaries of the somites. Mesoblast in that portion of the embryo that becomes the first segment (peristomium and prostomium) does not appear to split. Halving is possible from level of the somite that becomes segment ii well back towards the hind end.

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Biology of the Brook Stickleback Eucalia inconstans (Kirtland)

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In recent years the sticklebacks, especially *Gasterosteus aculeatus,* have been utilized as a tool for behavioral studies by the ethologists of Europe. Very little is known about the reproduction of the brook stickleback (*Eucalia inconstans*) and such information would be useful for a comparison with the behavior and ecology of other sticklebacks. The purpose of the present paper is to present field and laboratory observations that were made on this species in Michigan from 1952 to 1954 and to summarize the literature known to the author.

A few authors have reported that this species builds a nest and has habits similar to other sticklebacks (Bean 1903; Barker, 1918; Evermann and Clark, 1920; Adams and Hankinson, 1928; and others). Barker (1918) and Jacobs (1948), however, are the only authors that have published more than a note on field observations of the breeding habits of *Eucalia.* The present paper verifies and expands considerably the available information. As nearly as possible each subject will be taken up in the natural sequence of events of the stickleback. In only the detailed laboratory data will the new information be segregated from the known information on this fish.

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Localities and Methods

During 1952, 1953, and 1954 field observations were made in Sylvan Ponds in the Waterloo Recreation Area, T2S, R3E, S.6, Washtenaw Co., Michigan. These are small, spring-fed, impounded ponds used at times to hold trout and other game species. There was a thick growth of *Chara* sp. and algae in the ponds along with sticks, leaves, and other organic debris, and the bottom was silt and gravel. A few observations were made in a small spring-fed creek, on Packard Road between Ypsilanti and Ann Arbor, 1.5 miles east of U.S. Route 23, where the creek flowed through the Country Club Golf Course, R7E, T3S, S.6-7, Washtenaw Co., Michigan. It contained leaves, sticks, higher aquatic plants, and algae over a bottom that was heavily silted in most places.

Individuals from Sylvan ponds and the creek were placed in several tanks in the laboratory. The activities in one particular tank, Tank A, were observed in some detail. The tank was 45 x 25

x 30 cm high, and set in a shallow tap water bath. *Vallisneria* sp. was placed in one corner; *Chara* sp. was placed in another corner; and various sticks, pieces of leaves, and algae were added on top of the gravel bottom. On May 12, 1953 at 9:00 P.M., two ripe male and two ripe female sticklebacks were placed in the tank. The history of these individuals will be followed in some detail because reproduction was completed and could be carefully observed. The laboratory notes have been abbreviated and rephrased.

In order to induce the brook stickleback to breed in the laboratory the temperature was maintained several degrees below room temperature. Other items such as adequate space, nest materials and a nest site were properly supplied. In Tank A the temperatures were between 16 and 17°C except for the first day (19°C) and the last one or two days (18°C). In a second tank where limited spawning success was obtained the temperature varied from 17 to 18.5°C. Other sticklebacks kept at temperatures ranging from 19.5 to 24°C did not breed. In one instance a nest was started but never completed and in another, eggs were laid in a completed nest, but they were destroyed by the sticklebacks themselves before the reproductive cycle was completed. In the other aquaria at these higher temperatures there was no sign of nest building or sequential breeding behavior. Adams and Hankinson (1928) reported that several authors were not able to spawn this species in aquaria. It appears as though this is not true if the temperatures are kept at least several degrees below 20°C.

HABITAT

Various authors have reported the habitat of *E. inconstans* to be small streams, ponds, alkali lakes, spring holes, and swampy margins and beach ponds of larger lakes (Bajkov, 1930; Barker, 1918; Cox, 1922; Evermann and Clark, 1920; Hankinson, 1916; Hubbs and Lagler, 1947; and Miller, 1957). These fish live in waters characterized as cold, clear, and heavily vegetated. The small stream, Sylvan Ponds, and several places along the shore of Lake Michigan where sticklebacks have been noted were all spring-fed. Miller (1957) reported this stickleback to be common in the potholes of Alberta which are spring-fed lakes. Other localities in southern Michigan known to the author where the brook stickleback was common also were spring-fed. Trautman (1957) reported the occurrence of this species as common in spring-fed areas of northeast Ohio. This represents its southern limit at that point. The most notable factor correlated with springs is a low temperature. It appears that temperature limits the southern distribution and habitat of *E. inconstans*. The few isolated populations of northern Ohio and southern Michigan may represent remnants of more widespread populations present during the Pleistocene. Unless it becomes climatically colder in these areas one can visualize the southern boundary of the range as slowly moving northward due to man's activities and climatic warming.

AGE, FOOD, PARASITES, AND PREDATORS

Jacobs (1948) stated that sexual maturity was attained in one year. An impression of the size categories in Sylvan Ponds suggests that the population was made up mostly of one-year-old, some two-year-old, and possibly a few three-year-old fish. The ponds were poisoned with rotenone in the fall of 1952. A small population was still present the next spawning season. However, the next or second spawning season after poisoning the population attained its original density. This fact supports the idea that sexual maturity is attained in one year.

A large number of notes have been recorded on food items (Adams and Hankinson, 1928; Clemens, *et al.,* 1924; Evermann and Clark, 1920; Forbes, 1883; Greeley, 1927; Hankinson, 1916; Pearse, 1918; Pettit, 1902; Toner, 1933; and Woolman, 1895). It is concluded from these reports that this fish is carnivorous. A wide variety of aquatic insects (especially larvae) and crustaceans are the principle food items. Other items mentioned are as follows: snails, water mites, algae, fish eggs (their own and others), and oligochaetes. Although a considerable number of statements have been made about the brook stickleback eating fish eggs, the actual data demonstrate that these are a minor dietary item.

Various studies have pointed out that the stickleback is preyed upon by some fish and birds but usually is only a minor food item. Various predators are as follows: bowfin (Lagler and Hubbs, 1940), yellow perch, largemoth bass (Evermann and Clark, 1920), northern pike (Hunt and Carbine, 1951), pikeperch (Maloney and Johnson, 1957), brook trout (Ricker, 1930), belted kingfisher (Salyer and Lagler, 1949), laughing gulls and common terns (Pope, 1909).

The following parasites have been recorded for *E. inconstans:* TREMATODA — *Bunoderina eucaliae, Crepotrema funduli, Neascus* sp., *Tetracotyle* sp., *Gyrodactylus eucaliae; Diplostomum baeri eucaliae;* CESTODA — *Proteocephalus* sp.; NEMATODA — *Agamonema* sp., *Contracaecum* sp., *Rhabdochona cascadilla, Spinitectus gracilis, Spiroxys* sp.; ACANTHOCEPHALA — *Neoechinorhynchus rutili, Neoechinorhynchus* sp., *Leptorhynchoides thecatus* and *Pomphorhynchus bulbocolli* (Bangham, 1937; Bangham and Hunter, 1939; Fischthal, 1947, 1950, 1952; Hoffman and Hundley, 1957; Hoffman and Hoyme, 1958; Ikezaki and Hoffman, 1957).

MIGRATION AND REPRODUCTIVE PERIOD

Characteristically the brook stickleback migrates into shallow water to spawn in the spring, after which it gradually moves to deeper water or downstream in the summer. Applegate and Brynildson (1952) recorded a downstream movement during the fall and winter in northern Michigan, and Evermann and Clark (1920) said they were found in deeper water among vegetation in the summer, and in shallower water in winter and early spring. There is only a minimum of information on these movements.

Eucalia spawns in southern Michigan from late April or early May to the middle of June, but in northern Michigan they complete spawning about one month later. Nests with eggs were at least present in May and early June in Sylvan Ponds. Although over 25 nests were seen June 5 and 6, only 8 could be located on June 15, 1952, at which time all the eggs were well developed. In the same ponds during 1953 nests with non-eyed eggs were located on May 17 and nests were still present on the first of June. A few nests, with and without eggs, were found May 9, 1954. In the creek, nests were not found (May 12 and 16) until May 18, 1953 and none were found after June 15. Nests were seen in northern Michigan in early July near the Michigan Biological Station, Emmet Co. and by the shore of Lake Michigan near Cross Village, Emmet Co., on July 6, 1952. Temperatures recorded when nests were found were normally 15 to 19°C. In several situations just at the end of the nesting season temperatures rose to 27°C. Successful reproduction in aquaria occurred at 16 to 18°C. Barker (1918) stated that in central New York nesting begins at 40 - 50°F (5 - 10°C) and ends at 70°F (21°C) during April and May. According to Jacobs (1948) nesting begins in late March or early April and continues until June in the southern half of Minnesota. He further stated that the water must attain a minimum of 8°C before spawning begins. Harkness and Ricker (1929) found nests and eggs on July 1 in Ontario, Canada. From the above data it appears that spawning occurs later in more northerly latitudes as is generally true for many of our northern temperate freshwater fishes.

COURTSHIP, SPAWNING AND CARE OF EGGS

These subjects are divided into two main sections. One section describing observations in the laboratory presents a complete sequence of reproductive events in a situation where close accurate observations could be made. A second section relates our observations to those of other workers, discusses, and summarizes the activities.

OBSERVATIONS ON TANK A

The conditions of this tank are given under localities and methods.

May 12, 1953, 9:00 P.M.—Two ripe males and females placed in tank. Males were a light color like the females.

May 13, 9:00 A.M.—One male was almost jet black. This one is referred to as R male because he built a nest in the right side of the tank. The other is L male, in the left side of tank.

10:30 A.M.—Both males were almost jet black. One female was light colored and the other was black and gray-green variegated. Male R chased the light female who went to the bottom. The variegated female was near the surface. When the tank was disturbed, male R lightened in color but immediately darkened when he had a brief fight with the other male.

12:30 P.M.—Male R picked up a small piece of plant and carried it for a few seconds.

1:15 P.M.—Several sticks were added to the tank.

2:00 P.M.—The first piece of plant was attached to a stick within the next half hour.

4:15 P.M.—Male R had a few pieces of root and alga attached to a stick on the right side of the tank.

9:00 P.M.—Male R now had attached enough material to the crotch of a branch so that the outline of a nest was discernible. The males chased the females when they came near. Male R with a nest defended the right side of the tank and male L without a nest defended the left side of the tank. Male R chased a female into male L's territory twice. This carried male R into male L's territory from which male R was chased. Several times male R chased other fish. Male R attacked a finger placed near the nest. Active movement by the observer resulted in the male becoming temporarily lighter. Male R mouthed several pieces of alga before he placed them individually onto the nest. Then the male encircled the nest in many directions poking his snout at it and slightly pushing at material attached to the nest. Thus far mostly alga with only a few small pieces of roots had been used. He picked up a long strand of alga and moved his mouth over it and then spit it out. This action was repeated many times with some material put in the nest and some pieces rejected.

9:30 P.M.—Lights turned out. After one hour a light was turned on. The male was beside the nest and in a few seconds began to move rapidly.

May 14, 6:45 A.M.—The nest was completely formed but the male still added material to it. He may have worked at night. Male L has not attempted to start a nest. Another stick was added to L's territory. The nest (R) has only one hole and the male put his head in it several times. This pushing of the head kept an open space inside the nest and maintained the circular form of the hole. The male picked up many pieces of material some of which was rejected and some of which was added to the nest. Between these acts he curved his body to the contours of the nest and moved over its surface. Frequently he circled the nest "as though looking at it." The abdomen of one female was no longer enlarged. She may have released her eggs outside the nest. She was removed. Male R entered male L's territory and promptly was chased out.

1:00 P.M.—Another observer noted nest-building activities similar to those described above. One piece of plant was brought out from inside the nest, held in the male's mouth, and then was spit out.

9:30 P.M.—Nest-building activities and territorial chases were observed.

May 15, 9:00 A.M.—The remaining female was removed because she was thin and had apparently released her eggs outside of the nest. She was no longer variegated. The male added no material to the nest but spent most of his time poking his head inside the nest hole.

May 16, 2:30 P.M.—Two ripe females were added (2 females and 2 males now present). One went near male R and he attacked her vigorously. He hit her body with his snout several times until she left. Then he went to the nest and touched his mouth around the rim of the nest. Male L hit each female

as she entered his territory. Soon the females were chased from territory to territory. Male R swam into male L's territory and was chased, but as soon as he re-entered his own territory he stopped and turned. Male L did not enter male R's territory. The two males fought briefly at the boundary area. It appeared as though the R male placed some white fluid over the rim of the nest. This was done by touching the nest with the urogenital area. This was presumed to be the kidney secretory material used in binding the nest materials together. The male now spent considerable time mouthing the nest whereas the females, which had changed from a dark variegated appearance to a relatively uniform coloration, were hidden under the alga and in plants. The male R bit at several pieces of alga.

May 17, morning—Male R chased the now variegated females several times. There were eggs in the nest now, but a second hole, which would have been produced by the female as she swam through the nest, was not present. The male must have patched up the second hole. Male R stuck his head in the hole, pulled his head out, and wiggled in front of nest opening, moving the pectoral fins back and forth. This caused an observable current of water to pass over the eggs. The male fanned the nest briefly several times. In between times the male went around the nest poking his head at it. Two ripe females were added to the tank (4 females now in tank, one spent).

7:00 P.M.—Male R frequently chased ripe females, the spent female, and male L and in between he fanned eggs. Male L also chased females. Occasionally both males nipped at the females. Once, male L grabbed the pectoral fin of a female. The males acted as though an invisible line or very narrow space divided their territories. Once over this boundary a chased male stopped fleeing. He would turn and attack if the other male crossed over. Male R seemed much more vigorous in his attacks. In abbreviated form, what follows is a description of fifteen minutes activity by male R minute by minute: minute (1) head in nest, fanned eggs, chased females, fanned, chased female; (2) fanned, chased female; (3) head in nest, fanned; (4) head in nest, fanned; (5) repaired nest; (6) repaired nest, chased female; (7) head in nest, fanned; (8) fanned, chased female, chased female; (9) head in nest, fanned; (10) head in nest, fanned, chased female; (11) head in nest, fanned, chased female; (12) fanned, head in nest, fanned; (13) repaired nest; (14) head in nest, fanned, chased female; (15) chased female, fanned, chased female. This demonstrates the rapidity of activities by the nest-guarding male. The fanning of the eggs lasted from 1 to 3 seconds.

May 18, 8:30 A.M.—Male R vigorously chased females, poked head in nest, fanned eggs, and "inspected" nest several times within a few minutes. More eggs were in nest. Small pieces of a white substance were evident on nest and on bottom of tank.

1:00 P.M.—One gravid female was added to the nest (5 females in tank). Male R reacted as follows: went to her and bit her tail; bit again and she went to bottom; male placed head in nest and fanned eggs; went to female; bit and chased her actively; fanned eggs; and chased her again.

7:00 P.M.—Three partially spent females were removed and one ripe female added. This left three ripe females in the tank. Male R attacked and bit the net and a finger placed in the tank.

9:00 P.M.—One female was in the nest with her head sticking out of the nest opposite the regular opening. Observer chased her out. She came back to

nest area and male R attacked her once. She did not flee. The male went then to the entrance of nest. She followed and entered nest. Observer chased her out again. The male then moved eggs in the nest and fanned them. It appeared as though this kept an empty space in the nest as eggs were pushed to the side and down. The female came near the nest again. The male immediately went to the entrance of the nest and back to her. Observer chased her away. The male attacked her, she did not move and he then went to nest entrance. She entered nest. The male nudged his snout against the female's caudal peduncle. After 7 nudges the female vibrated vigorously; 2 nudges by male and the female vibrated again; and she vibrated again after three nudges. The female after 4 minutes then swam out the back side of the nest. The male immediately swam through the nest after her with only a brief pause over the eggs. It is presumed that the eggs were fertilized when the male went rapidly through the nest. The male then chased the less plump female out of his territory. He put his head in the nest and arranged the eggs by pushing them to the side and bottom. Male L was not as dark as male R.

May 19, 7:30 A.M.—Nest repair, egg-fanning, and territorial defense activities were observed.

May 20, 3:30 P.M.—A female was in the nest and the male poked at her caudal peduncle. During the fifteen-minute period in the nest she vibrated vigorously sixteen times. When she left the nest the male passed through the nest vibrating vigorously with only a seconds' pause inside the nest.

May 21—Nest R was much larger than when first completed, and, in fact, much larger than any comparable nest found in the field. Egg-fanning was observed.

May 22, 7:40 A.M.—The male added some material to the nest and the usual activities were observed.

May 24, 8:30 P.M.—Male L had built half of a nest. Two ripe females were added. The new nest was tied to two sticks, a *Vallisneria* frond and a bladderwort branch. It consisted of a few roots, a few bits of plants and mostly algal pieces. Male R still added material to his nest. An algal covering can be seen over the eggs inside the entrance. Male R performed his usual activities. The largest female nipped at the other females. A ripe female was now in the black variegated color pattern.

May 25, 11:15 A.M.—Male L now had a larger nest with eggs in it and he was fanning at the nest entrance for the first time.

May 26, morning.—The first young were observed at male R's nest around the entrance and on the surface of the nest. The male was fanning eggs at intervals of 4 to 6 seconds, which was an increase over the periods of 1 to 3 seconds first observed. There was also an increase in the frequency of fanning. The male dashed from place to place around the nest and poked rapidly at various parts of nest but did not add any material to it. The number of times a male fanned eggs was counted for 6 periods of five minutes each with the following results: male R, 8, 8, 9, 10, 9, and 10; and male L, 1, 3, 1, 2, 2, and 2. Almost every time male L fanned his eggs he also poked his head into the nest which resulted in the eggs being pushed to the side of nest. Male R with young did this about once out of every three times that he fanned the eggs. Eight larval fish (*Etheostoma nigrum*) introduced near male R were not eaten, whereas of ten larvae dropped near two males guard-

ing only eggs six were eaten. *Daphnia* and white worms were eaten by all males.

May 26, 7:00 P.M.—Movements of the young were observed. One went to the surface of the water and dropped back down on the outside of the nest near another larva. Male R came up, drew both young into his mouth, put his head into the nest and spit them out. He picked up two more young and spit them into the nest, which by now was somewhat deteriorated. He did the same with another larva and then pushed a piece of material against the nest. One larva swam to the surface and the male took him in his mouth. A female approached and the male postured at her by placing head downward and erecting the pelvic spine on her side. Then he spit the larva into the nest. At this point a series of experiments were carried out where individual larvae of *Etheostoma nigrum* were dropped near the L and R male sticklebacks. The results are given in Table I and will be discussed in the next section. The male had been actively grabbing his larvae and spitting them into the nest. The male took one dead larva out of nest and spit it out.

8:30 P.M.—The male has fanned the eggs and spit many young into the nest, but the young swam from the nest almost as fast as the male could retrieve them.

9:30 P.M.—The lights were turned out for five minutes. When the light was turned on, the young were seen scattered all over the tank and three females were near male R's nest. He immediately chased them away.

May 27, morning.—Male R spit many young into the nest. One female in the black variegated color pattern tried to get into R's nest. Many more young were outside of the nest than previously.

5:00 P.M.—An aggregation of young formed in the water above the nest. Many young were still on and in the nest.

7:00 P.M.—All or most of the young had been put back in the nest. When a flashlight was turned on a few larvae became active, but they were grabbed immediately by male R and spit into the nest. He repeated this action well over 100 times between 7:00 P.M. and 8:30 P.M.

May 28, 8:30 A.M.—A large aggregation of larvae were seen above the nest and many were seen on and in the nest. The male occasionally picked up one and spit it into the nest, but when he did this 2 to 5 other young came out of the nest. The male defended his territory actively any time it was entered by a female or by male L. Several times he chased a female when he had young in his mouth, but he did not bite her and immediately afterwards went to the nest and spit the young into it. The male usually picked up one larva and then spit it into the nest but several times two larvae were picked up and spit into the nest.

4:00 P.M.—The male occasionally spit larvae, one, two or three at a time into the side of the nest which by now consisted of just a mass of disorganized alga, but most of his time was now spent in territorial defense.

6:30 P.M.—Many larvae were in, on, and above the algal mass. The male continued to pick them up and spit them into the nest. The numbers picked up and spit into nest were as follows: 20 times one larvae picked up; 5 times two; and once three and once four. There were no eggs in the nest. Occasionally he stopped to attack an intruder. He returned 38 young to the nest

in 15 minutes (27 retrieving acts). It was almost dark. The first young were taken from the outskirts of the territory. When they were in the nest he started retrieving those in an aggregation above the nest. The young did not come out of the alga as they had during the day.

9:00 P.M.—Most of the young were in the algal remains of the nest.

May 29, morning.—The nest was no longer recognizable. The male circled the young occasionally and picked up a few and spit them into algae near where the nest was once located.

May 30.—Many young were scattered all over the tank.

June 1.—Males still maintained territories. Many young have disappeared.

June 3, 7:00 P.M.—First young seen in male L's nest.

June 4, 12:00 Noon.—Many young were around L nest.

7:30 P.M.—The nest was already slightly deteriorated and the male spit many young into the nest.

June 6, 1:00 P.M.—Male L was dying. Young have scattered throughout the tank. A few of male R's young were still present and male R still maintained a territory. (End of observations.)

SUMMARY AND COMPARISON OF OBSERVATIONS

Barker (1918) and Jacobs (1948) have given the following information on the breeding of the brook stickleback based on field observations: males were jet black during the spawning season; the male defended the nest which he built until the young hatched; the male fanned the eggs; female and male in an excited dance circled and butted until she entered the nest; then the male entered the nest to fertilize the eggs; male secreted material from the kidneys to glue the nest; and two or more females spawned in the same nest, laying up to 250 eggs or more each. The present observations expand upon the above and are essentially in agreement with them except on two points. It should be mentioned that it is assumed that the eggs were fertilized when the male passed through the nest. Also, it was assumed that the kidney secreted the material to glue the nest, although Jacobs *op. cit.* stated testes instead. The two points of disagreement are that the sticklebacks also guard the young after hatching (not just to hatching) and the description of an excited courtship dance by Jacobs *op. cit.* was not verified.

Almost all the activities observed in Tank A were also observed in the field with a greatly reduced frequency and in another aquarium.

First the males arrive in shallow water in the spring where they establish territories and start to build nests. Jacobs (1948) noted that a male may build two successful nests in one season. In the present observations some males were jet black before the nest was started and others became so only after the nest was completed.

The territories are defended against individuals of a reasonable

size of most species. Darters were attacked in aquaria and in the field. *Gambusia affinis* and a trout were chased. This defense was maintained both in the field and laboratory until after the young left what remained of the nest. Rather narrow boundaries existed between territories which the males were able to recognize. A male chasing another male often crossed his boundary and thus in turn was chased. If a male was in one side of his territory, an intruder male on the opposite side frequently penetrated more deeply into the territory before he was chased. Ritualized fights between males with spines erect were observed in the laboratory but infrequently in the field. One other fact was noted about the mapped territories in Sylvan Ponds. The ponds were poisoned between the 1952 and 1953 spawning season. The individual males of the much smaller 1953 population maintained larger territories. Furthermore, many males nested in the upper, middle and lower Sylvan Ponds in 1952. Only three or four nests were found in the upper pond, none in the middle and a fair number in the lower pond in 1953. All ponds had many males with nests in 1954. Only one year was required for the sticklebacks to attain their original population size.

In Sylvan Ponds while the males maintained territories and built nests the females swam in aggregations or individually outside of the males' area. Female dominance, noted in aquaria several times, was never observed in the field. When a female was ready to spawn her color changed from a uniform pale green to a variegated dark and light pattern. She then entered the male's territory where she was attacked. She responded in one of four ways to the male nips and butts. She moved toward the nest, remained motionless, went to the bottom, or moved on to another territory. If she remained still or went to the bottom, the male frequently would go to the opening of the nest. If she did not come to the nest, he would go back to her and the process was repeated. Several times nudges by the male appeared to direct the female towards the nest. Eventually the female entered a nest. In this position, with her head and tail sticking out each side of the nest, the male prodded her ventral region and her caudal peduncle. This resulted in her vibrating vigorously at which time presumably she laid eggs. After the female had vibrated, usually several to many times, she swam out of the nest where she was attacked frequently by the male. This does not seem to fit precisely Jacobs' (1948) brief descriptions of an excited courtship dance. She fled immediately to an area outside of the males' territories. Several times females attempted to enter nests too small for them so that the nests were partially destroyed. This fact would certainly select against individuals who had the tendency to build a nest too small.

The male cared for the nest by the continued addition of material and the repair of loose material. After eggs were laid in the nest, the male pushed them to the side and down. This left a space (through the center of the nest) across the nest and opposite the entrance. Barker (1918) reported that a male spit loose eggs at the entrance

into the nest. A male spent a great deal of time fanning his pectorals at the entrance of a nest with eggs. This activity increased in length of time and frequency as the eggs developed. A male with eggs was mainly occupied with repair of nest, arrangement of eggs, territorial defense and fanning of eggs. These were less frequent in the field than they were in Tank A (see May 17) probably because of the usually greater distances traveled in defense of a territory.

Finally after the eggs hatched, the male retained a territory around the tattered remains of the nest which swarmed with the larvae. This was apparently ended when the larvae swam fast and continuously enough so that the male was unable to retrieve them efficiently. For the first three or more days, the larvae spent a great deal of time in one position with their heads against the nest or other objects but at various angles to them. Larvae of *Etheostoma nigrum* were introduced to a male with only eggs and a male with eggs and young (Table I). The male with only eggs ate most of the dead and live larvae. The male with eggs and young retrieved most of the live ones and spit them into the nest whereas most of the dead ones were apparently disregarded. There is a distinct difference in approach between the two males and the underlying mechanism that causes the change needs to be investigated. The male with young could usually discriminate visually between a dead and live larva, yet he ate white worms and *Daphnia* at this time.

NESTS, EGGS, AND YOUNG

In general, the nests were roughly globular in shape and constructed variously of organic debris, algae and other materials. The nests were usually attached to a stem, on the bottom to over one foot

TABLE I.—Responses of male brook sticklebacks in Tank A on May 26 to larvae of *Etheostoma nigrum* when they were placed individually in the aquarium.

	No. Eaten	No. Disregarded	No. Inspected	No. Taken in Mouth and Spit out	No. Taken in Mouth and Spit in Nest
	Dead Larvae				
Male with young and eggs (Male R)	0	11	3	3	0
Male with only eggs (Male L)	13	1	0	1	0
	Live Larvae				
Male with young and eggs (Male R)	0	1	3	2	10
Male with only eggs (Male L)	5	0	0	0	0

above it. Barker (1918) reported finding nests of three quarters of an inch in diameter and fastened to a rootlet or grass blade. Jacobs (1948) said that the nests averaged 30 mm in diameter and were attached under cover to twigs or plant stems just above the bottom. The present observations expand upon these notes. The nests need not be under cover and diameters varied from 1.5 cm to 5 cm. They increased in size over the season as eggs were added and as the male added material to the nest. The bottom varied from organic debris to sand and various mixtures of both. In two years of observation at Sylvan Ponds, four nests were in contact with the bottom and forty were off the bottom although they were most commonly just off the bottom. Also, eight nests were found attached to the horizontal branch of a dead stem; four to logs, six to a vertical branch, 28 to vertical branches of live *Chara;* three to leaves; one to another vertical plant stalk; and 15 to dead horizontal stalks of plant stems. Some nests observed in Lake Michigan were attached to *Scirpus* stalks and to blades of grass bound together. Many more nests (80%) were found on *Chara* stalks in 1954 than in 1953 (5%). It could mean that sticks are preferred and the *Chara* is a second choice. The lowered population in 1953 resulted in mostly the use of sticks whereas many individuals of a greatly increased population in 1954 had to resort to the use of *Chara.* This will also vary according to the materials available and probably these variations can be greatly expanded when many populations over wide areas are investigated.

Barker (1918) said the nests were constructed of dead grass blades, fibers, etc., and later in the season, algae and seed sprouts. Jacobs (1948) reported nests made of plant pieces. Almost any sort of light small pieces of plant debris are used. Some of them found in this study were as follows: small sticks, pieces of many kinds of plants, *Chara,* duckweed and algae (very common).

Barker (1918) reported that in his study each nest had a single opening, while Jacobs (1948) stated that each nest had two openings. In the present study nests both with one and with two holes were found depending upon the occurrence of specific events. All the nests had one opening prior to the deposition of eggs by a female. She created a second hole upon leaving the nest through the side opposite the entrance maintained by the male. This second hole was repaired with varying degrees of success by the male, but such repair was observed much less often near the end of the spawning season. One nest was found with three holes in it, two of which were probably created by two different females.

Barker (1918) described the eggs as transparent and light yellow with a diameter of about 1 mm. He reported that the larvae hatched in eight or nine days at 20.5°C., were 5 mm in length at hatching and then attached by their head to various materials for the first few days. Jacobs (1948) reported that the eggs were 1.3 mm in diameter, colorless, and the young attached by the tip of the head possibly by means of a viscid spot. The eggs seen in this study were

as Barker described them and were also demersal and adhesive. The two sets of eggs observed in this study hatched as follows: 203 to 232 hours at 16° to 17°C and 220 to 259 hours at 17° to 18°C. The yolk sac was absorbed in about 100 hours. As for the young hanging by their head from objects, this could be explained by movements of the pectoral and caudal fins rather than by any viscid spot. The large number of observations made on this point will not be described because a definitive interpretation could not be made.

SUMMARY

The biology of the brook stickleback with emphasis on reproduction is described with the inclusion of all the literature available to the author at this time.

The brook stickleback lives in small pond-like areas and streams where the water is clear and where heavy vegetation occurs. It is restricted essentially to spring-fed areas in Ohio and southern Michigan.

The fish mature in one year, eat primarily insects and crustaceans and are eaten occasionally by some fish which are listed.

The fish migrate to shallow water to spawn in April, May and June at temperatures between at least 15° and 19°C. The nesting period starts later in the season north of southern Michigan.

A detailed description is given of their reproductive activities under laboratory conditions. This is then broadened to include field observations and those of other authors. The following activities are described: territoriality, nest building and repair, spawning, egg fanning, caring for eggs, and caring for young. Males with only eggs ate young larvae placed near them, whereas, males with young retrieved the larvae if alive and spit them into the nest.

The nests may have one or two holes. The second is produced by the female and variously repaired by the male. The nests are made of bits of dead organic debris and various pieces of live plants such as algae. The positions of nests are given and they are most often placed just off the bottom attached to some object. The eggs are described and hatching times given.

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Studies on the Trematode Family Brachycoeliidae. IV. A Revision of the Genus Mesocoelium Odhner, 1911; and the Status of Pintnaria Poche, 1907[1]

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This paper is the last of four concerned with the taxonomy of the trematode family Brachycoeliidae. Earlier ones (Cheng, 1958, 1959, 1960) dealt with the systematics of the genera *Brachycoelium* (Dujardin, 1845) Stiles and Hassall, 1898; *Leptophallus* Lühe, 1909; *Cymatocarpus* Braun, 1901; *Glypthelmins* Stafford, 1905; *Margeana* Cort, 1919; and *Reynoldstrema* Cheng, 1959. Their subfamilies were redefined by Cheng and Provenza (1960). The genus *Mesocoelium* Odhner, 1911, is discussed herein, and the monotypic *Pintnaria* Poche, 1907, is considered a synonym.

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The Genus MESOCOELIUM Odhner, 1911

The genus *Mesocoelium* was originally assigned to the subfamily Brachycoeliinae Looss, 1899 by Odhner (1911). Dollfus (1929) erected the subfamily Mesocoeliinae with *Mesocoelium* as the type genus, and later (1933) erected Mesocoeliidae to include this subfamily. Dollfus' system has not been widely accepted. The author, however, is of the opinion that in recognizing the family Brachycoeliidae Johnston, 1912, (see Cheng, 1959 and Cheng, 1960) Mesocoeliinae is of some systematic value as a subordinate group (Cheng, and Provenza, 1960).

The affinities between *Brachycoelium* and *Mesocoelium* are expressed in the morphology of the excretory vesicle, the flame-cell pattern, the general body outline and size, the location and ratios of the suckers, the shapes and relative sizes of the gonads, the distribution of the vitellaria, the specific category of hosts (*i.e.*, amphibians and reptiles), and the parallel life history patterns. In the opinion of the author, the differences in the relationship of the testes to the ovary and the comparative lengths of the intestinal ceca, justify the assignment of the two genera to separate subfamilies, Brachycoeliinae

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and Mesocoeliinae, an arrangement that Yamaguti (1958) has accepted.

Of the 32 described species of *Mesocoelium,* one, *M. sokolowi* Skrjabin, 1916, has been transferred to the genus *Anchitrema* by Dollfus (1929), where, in the author's opinion, it properly belongs. There is disagreement as to how many of the remaining species are valid, because they show marked morphological resemblances and have received little attention in recent years. An attempt is made here to clarify the matter by utilizing certain diagnostic characteristics which seem sufficiently consistent to be reliable.

The shape of the excretory vesicle apparently is useful in distinguishing species but is not known for all the species. Furthermore, in several instances the vesicle is Y-shaped but with extremely short cornua, making it debatable as to whether it is actually I- or Y-shaped. The author, therefore, has chosen not to rely heavily upon the shape of the excretory vesicle in separating species.

In the genus *Mesocoelium,* 3 distinct groups of species can be distinguished by the location of the testes. In the first group, which includes *M. sociale, M. microon, M. carli, M. meggitti, M. monodi, M. marrsi, M. danforthi, M. leiperi, M. crossophorum, M. schwetzi, M. maroccanum, M. lanceatum, M. elongatum, M. sibynomorphi, M. travassosi,* and *M. brachyenteron,* the testes are symmetrically placed on each side of the acetabulum; in the second group, including *M. ovatum, M. japonicum, M. americanum,* and *M. minutum,* the testes are anterior to the level of the acetabulum; and in the third group, including *M. incognitum, M. burti, M. mesembrinum, M. megaloon, M. oligoon, M. geoemydae, M. georgesblanci,* and *M. megrebense,* the testes are posterior to the level of that sucker.

The first group can be divided into 2 subgroups based on the length of the intestinal ceca. In *M. sociale, M. microon, M. carli, M. leiperi, M. travassosi, M. crossophorum, M. schwetzi, M. meggitti, M. monodi, M. marrsi, M. danforthi* and *M. maroccanum,* they extend past the midlevel of the body, whereas in *M. lanceatum, M. elongatum, M. sibynomorphi,* and *M. brachyenteron,* the ceca terminate before reaching that level and usually are confined to the anterior one-third of the body.

In the subgroup with longer ceca, species are distinguished by: (1) the position of the genital pore which may be median and at the esophageal level, or posterior to the intestinal bifurcation, or lateral and anterior to that bifurcation; (2) the configuration of the vitellaria; (3) the size and shape of the cirrus pouch; (4) the length of the esophagus; (5) the relative sizes of the testes to the acetabulum; and (6) the body dimensions.

Species in the subgroup with short ceca can be separated by (1) the distribution and configuration of the vitelline follicles; (2) whether the ceca extend posterior to the testes and/or ovary; (3) the size of the cirrus pouch; and (4) whether the genital pore is anterior or posterior to the intestinal bifurcation.

In the group with the testes anterior to the acetabulum, species differ in (1) the configuration and extent of the vitellaria; (2) whether the ceca extend beyond the level of the testes and/or ovary; and (3) whether the ovary is at the level of the acetabulum or posterior to it.

Species in the third group are distinguished by: (1) the sizes of the gonads; (2) whether the genital pore is anterior or posterior to the intestinal bifurcation; (3) size of the cirrus pouch; (4) length of the esophagus and intestinal ceca; and (5) configuration and extent of the vitellaria.

Mesocoelium emend.

Diagnosis.—With characters of subfamily Mesocoeliinae (see Cheng and Provenza, 1960); genital pore either anterior or posterior to intestinal bifurcation, on or lateral to midline; testes anterior to, on same level as, or posterior to acetabulum; uterus with much folded ascending and descending limbs, folds limited to post-ovarian area; intestinal parasites of amphibians and reptiles.

Type species.—Mesocoelium sociale (Lühe, 1901) so designated by Odhner (1911).

After evaluating all the reported species of *Mesocoelium*, the following are considered to be valid. All measurements are given in millimeters.

Mesocoelium sociale (Lühe, 1901) Odhner, 1911
Plate I, Fig. 1

Syn. *Distomum sociale* Lühe, 1901.

Diagnosis.—Body elongate, 2.8-3.5 long, 0.7-0.72 wide; cuticle spinous, spines more conspicuous in anterior half of body; oral sucker 0.275-0.34 by 0.27-0.32, acetabulum 0.185-0.32 in diameter; prepharynx present, pharynx 0.1-0.134 by 0.065-0.098; esophagus of medium length; intestinal ceca reaching posterior one-third of body; testes, 0.17-0.24 by 0.15-0.23, at sides of acetabulum, overlapping ceca; cirrus pouch slightly longer than diameter of testes; genital pore ventral, at midlevel of esophagus; ovary posterior to right testis, 0.18-0.225 by 0.17-0.18; vitellaria of large separated follicles from lateral margins of oral sucker to tips of ceca, never intercecal; excretory vesicle Y-shaped. Eggs 0.031-0.033 by 0.02-0.023.

Type host.—Bufo melanostictus.

Type locality.—India (exact location not given).

Type specimen.—Not extant.

Three specimens of *M. sociale* from Montevideo, Uruguay, resemble *M. monodi*. They can be separated from that species by the larger testes which are situated on each side of the acetabulum and overlapping the ceca.

Mesocoelium sociale has been reported from *Bufo melanostictus* in Indonesia by Odhner (1911), in Calcutta, India, by Sewell (1920), from Burma by Bhalerao (1936), from Rangoon, Burma, by Chatterji (1940) and Meggitt (1927), from *Bufo* sp. in Indonesia by Bhalerao (1936), from *Rana tigrina* in Rangoon, Burma, by Meggitt (1927),

PLATE I

Fig. 1.—*Mesocoelium sociale* (Lühe, 1901). Dorsal view (Redrawn after Odhner, 1911). Fig. 2.—*M. microon* Nicoll, 1914. Ventral view (Redrawn after Nicoll, 1914). Fig. 3.—*M. carli* André, 1915. (Redrawn after André, 1915). Fig. 4.—*M. meggitti* Bhalerao, 1927. Ventral view (Redrawn after Bhalerao, 1927). Fig. 5.—*M. monodi* Dollfus, 1929. Ventral view (Redrawn after Dollfus, 1929). Fig. 6.—*M. marrsi* Fernando, 1933. Dorsal view (Redrawn after Fernando, 1933).

PLATE II

Fig. 1.—*Mesocoelium danforthi* Hoffman, 1935. Dorsal view. Camera lucida drawing of type specimen. Fig. 2.—*M. leiperi* Bhalerao, 1936. Dorsal view (Redrawn after Bhalerao, 1936). Fig. 3.—*M. travassosi* Pereira and Cuocolo, 1940. Ventral view (Redrawn after Pereira and Cuocolo, 1940). Fig. 4.—*M. mesocoelium* (Cohn, 1903) n. comb. Ventral view (Redrawn after Dollfus, 1950). Fig. 5.—*M. crossophorum* Pérez, 1942. Ventral view (Redrawn after Pérez, 1942). Fig. 6.—*M. maroccanum* Dollfus, 1951. Ventral view (Redrawn after Dollfus, 1951).

PLATE III

Fig. 1.—*Mesocoelium lanceatum* Goto and Ozaki, 1929. Ventral view (Redrawn after Goto and Ozaki, 1929). Fig. 2.—*M. elongatum* Goto and Ozaki, 1929. Ventral view (Redrawn after Goto and Ozaki, 1929). Fig. 3.—*M. sibynomorphi* Ruiz and Leão, 1943. Dorsal view (Redrawn after Ruiz and Leão, 1943). Fig. 4.—*M. brachyenteron* Dollfus, 1954. Ventral view (Redrawn after Dollfus, 1954). Fig. 5.—*M. ovatum* Goto and Ozaki, 1930. Ventral view (Redrawn after Goto and Ozaki, 1930). Fig. 6.—*M. japonicum* Goto and Ozaki, 1930. Dorsal view (Redrawn after Goto and Ozaki, 1930).

PLATE IV

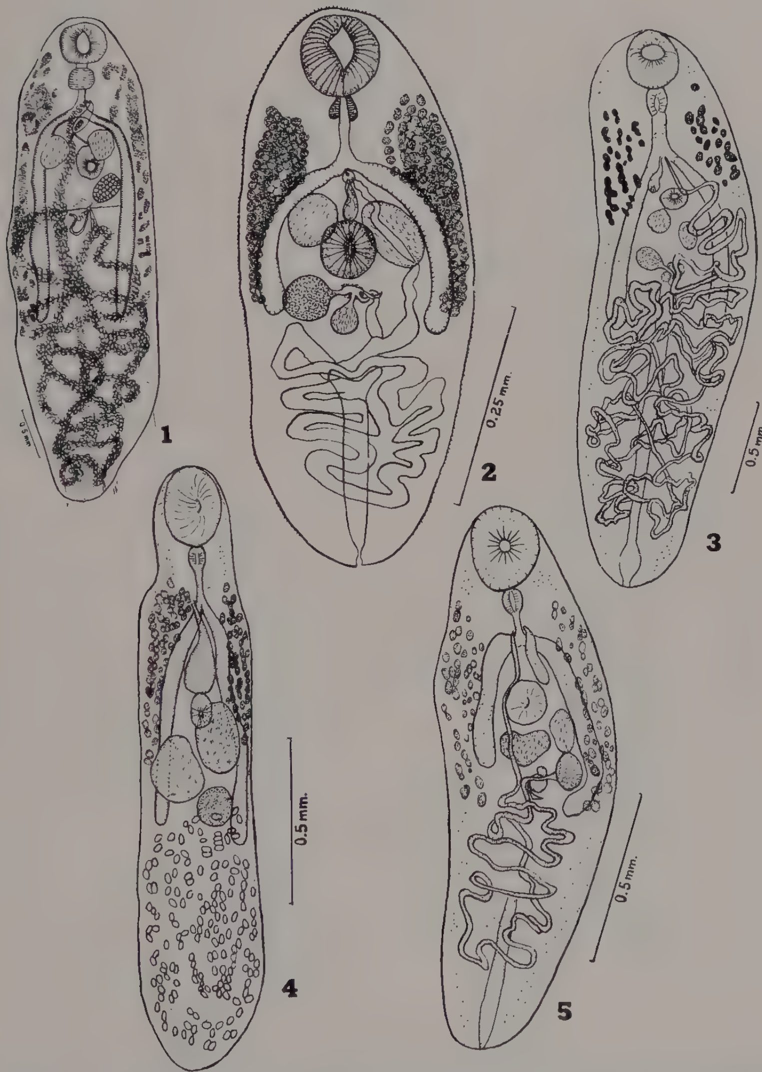

Fig. 1.—*Mesocoelium americanum* Harwood, 1932. Dorsal view. Camera lucida drawing of type specimen. Fig. 2.—*M. minutum* Park, 1939. Ventral view (Redrawn after Park, 1939). Fig. 3.—*M. mesembrinum* Johnston, 1912. Dorsal view (Redrawn after Johnston, 1912). Fig. 4.—*M. megaloon* Johnston, 1912. Ventral view (Redrawn after Johnston, 1912). Fig. 5.—*M. oligoon* Johnston, 1912. Dorsal view (Redrawn after Johnston, 1912).

PLATE V

Fig. 1.—*Mesocoelium incognitum* Travassos, 1921. Ventral view. Camera lucida drawing of type specimen. Fig. 2.—*M. burti* Fernando, 1933. Dorsal view (Redrawn after Fernando, 1933). Fig. 3.—*M. geoemydae* Ozaki, 1935. Ventral view (Redrawn after Ozaki, 1935). Fig. 4.—*M. georgesblanci* Dollfus, 1954. Ventral view (Redrawn after Dollfus, 1954). Fig. 5.—*M. magrebense* Dollfus, 1954. Ventral view (Redrawn after Dollfus, 1954).

from *Ptyas mucosus* in Rangoon, Burma, by Chatterji (1940), and from *Bufo crucifer* in Brazil by Travassos (1924).

Sewell (1920) reported the flame-cell pattern of this species to be 2 [(3+3+3)+(3+3+3)] which Faust (1932) gave as the pattern in the Dicrocoeliidae.

Mesocoelium mesembrinum Johnston, 1912
Plate IV, Fig. 3

Diagnosis. — Body elongate, 2.3-3.7 long, 0.89-1.6 wide; entire cuticle spinous; oral sucker 0.293 in diameter; acetabulum 0.196 in diameter; prepharynx not observed; esophagus of medium length; intestinal ceca reaching midlevel of body; testes oval, 0.195 in greatest diameter, posterior to acetabulum, oblique, with right testis slightly more anterior; cirrus pouch approximately as long as testes; genital pore ventral at intestinal bifurcation; ovary, 0.163 in greatest diameter, posterior to right testis; vitellaria of small separated follicles in lateral fields from level of pharynx to that of testes, never posterior to ovary; excretory vesicle I-shaped, extending to level of seminal receptacle. Eggs averaging 0.04 long by 0.025 wide.

Type host.—Hyla caerulea.

Type locality.—Nouveau Galles du Sud, Australia.

Type specimen.—Australian Museum Coll. No. W-341.

In the author's opinion, *Mesocoelium mesembrinum* is not synonymous with *M. oligoon* as considered by Pereira and Cuocolo (1940). The distribution of the vitellaria of *M. mesembrinum* is limited to areas lateral to the ceca from the level of the pharynx to the anterior one-fourth of the intestinal ceca; that ot *M. oligoon* is also lateral to the ceca, but extends posteriorly beyond the cecal tips. The left cecum of *M. oligoon* is longer than the right while the ceca of *M. mesembrinum* are of equal length. For these reasons the 2 species should be considered distinct.

Mesocoelium mesembrinum is similar to *M. georgesblanci,* but is distinguished from that species by the disposition of its vitellaria. The follicles are extracecal along the anterior one-third of the ceca and not along the entire lengths as in *M. georgesblanci.* Furthermore, the acetabulum, cirrus pouch, and gonads of *M. mesembrinum* are smaller and a conspicuous prepharynx is absent.

The only other record for the distribution of *M. mesembrinum* is that of T. H. Johnston (1916) who reported this species in the same host at Brisbane, Queensland, Australia.

Mesocoelium megaloon Johnston, 1912
Plate IV, Fig. 4

Diagnosis.—Body elongate, averaging 1.8 long, 0.358 wide; cuticle aspinous; oral sucker 0.194 in diameter, acetabulum 0.065 in diameter; prepharynx absent, esophagus moderately long, intestinal ceca extending into middle one-third of body; testes irregularly oval, averaging 0.182 by 0.129, slightly obliquely arranged, overlapping ceca laterally; right testis slightly more anterior and overlapping acetabulum dorsally; ovary subspherical, averaging 0.112 in diam-

eter, immediately behind and slightly to right of left testis; cirrus pouch, approximately twice the size of acetabulum, filling intercecal space anterior to acetabulum; genital pore on midline anterior to intestinal bifurcation; vitelline glands in lateral fields from level of esophagus to that of testes; excretory vesicle Y-shaped. Eggs 0.043-0.052 by 0.029.

Type host.—*Hyla ewingii.*

Type locality.—Sydney, Australia.

Type specimen.—Australian Museum Coll. No. W-343.

Mesocoelium megaloon appears to be most closely related to *M. georgesblanci,* which, however, has large testes (0.181 by 0.129) that overlap the ceca.

Mesocoelium oligoon Johnston, 1912
Plate IV, Fig. 5

Diagnosis.—Body elongate, averaging 1.53 long, 0.59 wide; cuticle sparsely covered with spines; oral sucker 0.215 in diameter, acetabulum 0.129 in diameter; esophagus of medium length; intestinal ceca unequal, left cecum extending posterior to level of ovary, right cecum reaching only to level of testes; testes irregularly oval or "polyhedral," averaging 0.165 by 0.099, side by side in intercecal region posterior to acetabulum; cirrus pouch long, slender, approximately as long as diameter of acetabulum; ovary oval, 0.133 by 0.09, situated posterior to left testis; vitelline follicles, 0.028-0.032 long, comparatively numerous, about 70 on each side, extending from level of pharynx to beyond tip of right cecum and to tips of left cecum; excretory vesicle I-shaped extending anteriorly through posterior one-fourth of body length. Eggs 0.039-0.052 by 0.028.

Type host.—*Hyla citropus.*

Type locality.—Lodden River (near Bulli), New South Wales, Australia.

Type specimen.—Australian Museum Coll. No. W-342.

Mesocoelium oligoon most closely resembles *M. megaloon,* but can be distinguished from the latter by its ceca which are characteristically unequal in length, by its testes which are smaller and which do not overlap the ceca, by its vitellarial configuration in extending along the entire lengths of the ceca and sometimes beyond them, and by its smaller cirrus pouch which does not occupy the entire intercecal space anterior to the acetabulum.

Mesocoelium microon Nicoll, 1914
Plate I, Fig. 2

Diagnosis.—Body elongate oval, 1-3.5 long, 0.77 wide; cuticle more spinous towards anterior end of body; oral sucker averaging 0.25 in diameter, acetabulum averaging 0.18 in diameter; no prepharynx reported, pharynx 0.08 in diameter, esophagus approximately twice the length of pharynx, intestinal ceca reaching past midlength of body, testes irregularly oval, 0.21 by 0.14, on same level as acetabulum, partially overlapping it dorsally along their median borders; cirrus sac slender, length approximates greatest diameter of testes; ovary posterior to left testis, averaging 0.15 in diameter; vitellaria of comparatively small follicles, laterally situated, from level of pharynx to cecal tips. Nicoll (1914) stated that the extent of the follicles were viable and may be

completely absent on one side posterior to acetabulum. Excretory vesicle I-shape extending anteriorly to midlength of body. Eggs 0.033-0.041 by 0.024-0.028.

Type hosts.—Hyla coerulea, H. gracilenta and *Tiliqua scincoides.*[1]

Type locality.—North Queensland, Australia.

Type specimen.—Unknown.

The author is not in agreement with Pereira and Cuocolo (1940) who considered *M. microon* as synonymous with *M. oligoon.* Examination of the original descriptions and plates by Johnston (1912) and Nicoll (1914) indicates that *M. microon* can be separated from *M. oligoon* by the position of the testes on the same level and on each side of the acetabulum in *M. microon* and by the equal length of the intestinal ceca. In *M. oligoon* the irregularly shaped testes are posterior to the acetabulum and the ceca are of unequal length. Until further evidence indicates differently, *M. microon* and *M. oligoon* must be considered distinct species.

Mesocoelium microon most closely resembles *M. carli, M. crossophorum,* and *M. monodi,* but it can be distinguished from *M. carli* by the extremely small independently follicular vitellaria, and by the position of its testes on the same level as the acetabulum. In *M. carli* the vitelline follicles are large and fused to form a continuous band; the testes are partially posterior to the acetabulum. *M. microon* can be distinguished from *M. crossophorum* by the medially placed genital pore anterior to the cecal bifurcation; by the smaller ovary which is not larger than the testes; and by the absence of refractile spicules along the anterior and lateral margins of the oral sucker. In *M. crossophorum* the genital pore is on the right of the esophagus and the ovary is larger than the testes.

Mesocoelium carli André, 1915
Plate I, Fig. 3

Diagnosis.—Body elongate, narrow at anterior and posterior ends; 0.88 long, 0.28 wide; oral sucker 0.086-0.095 in diameter, acetabulum 0.05-0.068 in diameter; no prepharynx observed, pharynx 0.025 in diameter; esophagus 2 to 3 times as long as pharynx; intestinal ceca extending to, or slightly posterior to midlength of body; testes globular, approximately same size as acetabulum, partially posterior to it and overlapping it along their anteromedial borders; ovary approximately same size as testes, posterior to and partially overlapping left testis; vitellaria extensive, follicles large, forming two continuous masses along extent of esophagus and ceca. André (1915) reported that the compact vitellaria may extend medially into the intercecal zone. Excretory vesicle Y-shape. Eggs 0.037-0.047 by 0.022-0.026.

Type host.—Cinixys belliana.

Type locality.—Busu, Uganda, Africa.

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[1] Nicoll (1914) reported *M. microon* as very common in the 3 hosts in North Queensland, Australia; a single host usually possessed 10-40 parasites in its duodenum; but he failed to mention from which of the 3 hosts the type specimen was recovered, hence all 3 are listed as the "type hosts."

Type specimen.—Not extant.

Other specimens.—Helminth. Coll., Museum of Natural History, Paris, France.

Mesocoelium carli most closely resembles *M. microon*, but it can be distinguished from the latter by its large, compactly fused vitelline glands. In *M. microon* the vitelline follicles are small and distinct.

Dollfus (1950) reported this species in *Cinixys erosa* from Port-Gentil, Gabon, Africa.

Mesocoelium incognitum Travassos, 1921
Plate V, Fig. 1

Syn. *Mesocoelium waltoni* Pereira and Cuocolo, 1940.

Diagnosis.—Body elongate, 1.151-1.249 long, 0.5-0.9 wide; cuticle beset with spines in anterior half or two-thirds of body; oral sucker 0.14-0.25 in diameter, acetabulum 0.16-0.3 in diameter; no prepharynx, pharynx 0.06-0.1 in diameter; esophagus short, less than length of pharynx; intestinal ceca reaching posterior one-third of body; testes irregularly oval, close to and posterior to acetabulum, right testis, 0.062-0.18 by 0.053-0.101, slightly anterior to left, left testis 0.08-0.164 by 0.049-0.113; cirrus pouch small, approximately half the diameter of acetabulum in length; ovary irregularly oval, 0.082-0.2 by 0.049-0.147, posterior to left or right testis; vitelline follicles small and sparsely arranged, from lateral borders of oral suckers to cecal tips; excretory vesicle Y-shape, extending to level of cecal tips. Eggs 0.037-0.041 by 0.021-0.025.

Type host.—*Bufo marinus.*

Type locality.—Guaratinguetá, Brazil.

Type specimen.—Helminth. Coll. Institudo Oswaldo Cruz, San Paulo, Brazil.

Four specimens of this species from Sao Paulo, Brazil, were studied.

Pereira and Cuocolo (1940) described *Mesocoelium waltoni* from the intestine of *Bufo marinus* captured at San Paulo, Brazil. These authors stated that *M. waltoni* closely resembles *M. megaloon* Johnston, 1912, and *M. carli* André, 1915. However, the species can be easily distinguished from one another by the sizes and arrangements of the vitelline follicles, which are larger and more compact in *M. carli*, medium-sized and not compact in *M. megaloon*, and extremely small and comparatively more sparse in *M. waltoni*. Furthermore, the relative positions of the testes and ovary also serve as diagnostic characteristics. Further study revealed that *M. waltoni* is identical with *M. incognitum* Travassos, 1921. The dimensions of the body, suckers, gonads and other internal organs vary within the same size range. The relative positions of the internal organs, the configuration of the vitellaria, and the type of excretory vesicle, are all identical, even the positions of the cornual bifurcation of the Y-shaped excretory vesicle. The fact that both were recovered from the same host, *Bufo marinus*, from Brazil, further suggests the probability of their being identical.

Mesocoelium incognitum most closely resembles *M. geoemydae* although the morphological similarity is not great. *M. incognitum* (body length 1.15 - 1.25 mm) is shorter than *M. geoemydae* (body

length 1.55 - 1.85 mm); the diameter of the acetabulum of *M. incognitum* may be as large as 0.3 mm, while that of *M. geoemydae* is never larger than 0.12 mm; and the vitelline follicles of *M. incognitum* are extremely small and are scattered in the lateral fields in the anterior two-thirds of the body, while those of *M. geoemydae* are larger in size and are limited to the region along the lateral margins of the ceca.

The only other record of *Mesocoelium incognitum* is that of Travassos (1924) in *Bufo crucifer* from San Paulo, Brazil.

Mesocoelium meggitti Bhalerao, 1927
Plate I, Fig. 4

Diagnosis.—Body elongate, broader anteriorly than posteriorly, 1.02-3.3 long, 0.36-1.03 wide; cuticle spinous in anterior half or two-thirds of body; anterior sucker 0.14-0.27 in diameter, ventral sucker 0.07-0.17 in diameter; prepharynx present, pharynx 0.05-0.1 by 0.06-0.13, esophagus short, 0.02-0.08 in length; intestinal ceca reaching posterior one-third of body; testes oval, 0.08-0.2 by 0.07-0.15, one anterior to its mate, on each side of acetabulum; cirrus pouch small, 0.23 by 0.10; genital pore at midlength of esophagus but to left of midline, ovary suboval, 0.08-0.2 by 0.07-0.15, posterior to anteriormost testis; vitelline glands singularly follicular, lateral, from level of anterior sucker to near ends of ceca; excretory vesicle I-shape. Eggs 0.03-0.036 by 0.02-0.024.

Type host.—*Mabuia dissimilis.*

Type locality.—Rangoon, Burma.

Type specimen.—Unknown.

Chatterji (1931) reported this parasite from the same host from India, while Tubangui (1931) reported *M. meggitti* in *Mabuia multifasciata* from Los Ranos, Philippine Islands.

Mesocoelium meggitti most closely resembles *M. maroccanum*. Both species possess a genital pore which opens ventrally to the left of the median line; however, *M. meggitti* can be distinguished from *M. maroccanum* by its larger gonads, the greatest diameter of the testes is subequal to that of the acetabulum, while the ovary is as large, if not larger, than the testes. In *M. maroccanum* the testes are approximately one-fourth the size of the acetabulum, and the ovary is proportionally smaller.

Mesocoelium lanceatum Goto and Ozaki, 1929
Plate III, Fig. 1

Syns. *Mesocoelium brevicaecum* Ochi, 1930.
Mesocoelium pearsei Goto and Ozaki, 1930.

Diagnosis.—Body lanceolate, narrower at posterior end, 2.0-3.3 long, 0.52-0.95 wide; cuticle spinous in anterior half of body; oral sucker 0.22-0.33 in diameter, acetabulum, 0.15-0.24 in diameter, situated in anterior one-fourth of body; prepharynx very short, pharynx 0.07-0.09 in diameter, esophagus 0.18-0.24 long; intestinal ceca comparatively short, only reaching level of posterior margins of testes; testes suboval, 0.10-0.29 by 0.07-0.22. on same place and on each side of acetabulum, partially overlapping the latter; ovary, 0.12-0.17 in diameter, posterior to right testis; cirrus pouch small, 0.021-0.027 by

0.08-0.1; vitellaria of singular follicles mainly lateral to esophagus and ceca but some follicles intermingle along medial line; excretory vesicle Y-shape. Eggs 0.04-0.051 by 0.023-0.031.

Type host.—*Tylototriton andersoni.*

Type locality.—Hyukyu Islands, Japan.

Type specimen.—Not available.

Goto and Ozaki (1929) first mentioned *Mesocoelium brevicaecum* (*nomen nudum*) which was not described until 1930 by Ochi from the intestine of *Bufo vulgaris formosus* from Hiroshima and Otsu, Japan. Ono (1930) reported this species in the same host and also in *Elapha quadrivirgata* and *Rana catesbiana,* captured at Onomichi, Japan; and Yamaguti (1936) reported *M. brevicaecum* from the type host at Kyoto, Japan.

The author believes that *M. brevicaecum* should be considered synonymous with *M. lanceatum* Goto and Ozaki, 1929. The body dimensions of the two species fall within the same range; the arrangement of the cuticular spines are identical. The testes of *M. brevicaecum* (0.10 - 0.24 by 0.07 - 0.10 mm) are slightly smaller than that of *M. lanceatum* (0.2 - 0.29 by 0.2 - 0.22 mm), but the greater dimension is in width only and the difference is insignificant; the ovaries are within the same range and so are the eggs. The distribution of the vitellaria are similar and both species have the Y-type excretory vesicle. Goto and Ozaki (1929) realized the great similarity between the two species and apparently had knowledge of the existence of Ochi's specimens, but erected *M. lanceatum* based on differences in body outline, ratio of suckers and coiling of the uterine limbs. These highly variable characteristics can all be attributed to the degree of contraction during fixation.

Ochi (1930) reported the life cycle of *M. brevicaecum* (=*M. lanceatum*). The fluke utilizes only one intermediate host, the land snail, *Euhadra quaesita* (Deshayes), and the cercaria, in the molluscan host, develops into an unencysted metacercaria for which Ochi used the term "adoluscaria." This life history pattern is essentially identical to that of *Brachycoelium obesum* Nicoll, 1914 (Cheng, 1960). This information serves as further evidence that *Mesocoelium* and *Brachycoelium* are closely related. In a report of the life history of *Glypthelmins quieta,* Rankin (1944) pointed out the phylogenetic proximity of *Glypthelmins* to *Brachycoelium* and hence also to *Mesocoelium.* The parallel life cycles must be considered of great importance and strong evidence for the grouping of these genera under the independent family, Brachycoeliidae.

Pereira and Cuocolo (1940) considered *M. brevicaecum* and *M. ovatum* both synonymous with *M. elongatum.* The author is not in agreement with these designations since *M. brevicaecum* (=*M. lanceatum*) can be easily separated from *M. ovatum* by the relative sizes of their gonads. In *M. brevicaecum* the testes are approximately one-third the size of the acetabulum and are situated on each side of it, while in *M. elongatum* they are similarly situated but are approxi-

mately the same size as the acetabulum; furthermore, the cirrus pouch of *M. brevicaecum* is as long as the diameter of the acetabulum, while in *M. elongatum* the cirrus pouch is approximately twice as long as the diameter of the acetabulum.

M. ovatum differs from *M. elongatum* by its smaller cirrus pouch the length of which is approximately two-thirds the diameter of the acetabulum; by the position of its testes, distinctly anterior to the acetabulum. In *M. elongatum* the length of the cirrus pouch is approximately twice the diameter of the acetabulum, and the testes are approximately the same size (and on the same level) as the acetabulum.

Until further evidence can be provided through life history studies, these morphological differences must suffice in the retention of *M. ovatum* and *M. elongatum* as distinct species and, for the reasons given above, *M. brevicaecum* is considered a synonym of *M. lanceatum*.

In 1930 Goto and Ozaki described *Mesocoelium pearsei* from the small intestine of *Pseudosalamandra stejnegeri* (Dunn) from Kagoshima, Japan. They stated that this species is closely related to *M. elongatum* Goto and Ozaki, 1929, but could be distinguished from it in that "the body is somewhat broader, the oral sucker and the acetabulum are closer to each other, and the intestinal ceca extend beyond the acetabulum." These characteristics are among those which separates *M. lanceatum* from *M. elongatum*. The author is of the opinion that *M. pearsei* is identical with *M. lanceatum*. The body dimensions of the two species fall within the same range; the alimentary tracts appear to be identical; the gonads and related structures are situated in identical positions; however, the testes of *M. pearsei* are slightly smaller than those of *M. lanceatum* (a difference of 0.07 mm which may be attributed to the differences in pressure during fixation) but this can hardly be considered valid as a species characteristic. Furthermore, the vitellarial patterns, positions of the genital pores, sizes and positions of the suckers and the dimensions of the eggs are all comparable. For these reasons the author considers *M. pearsei* synonymous with *M. lanceatum*.

Pereira and Cuocolo (1940) suggested that *M. pearsei* is synonymous with *M. japonicum*, a decision based on morphological similarities. The author does not agree since the two can be easily distinguished by the intestinal ceca which extend posterior to the level of the ovary in *M. japonicum* and are shorter in *M. pearsei*. Furthermore, the testes of *M. pearsei* are on the same level as the acetabulum while those of *M. japonicum* are anterior to the acetabulum. For these reasons, the author does not accept Pereira and Cuocolo's designation, but, as indicated above, considers *M. pearsei* a synonym of *M. lanceatum*.

Mesocoelium lanceatum most closely resembles *M. brachyenteron*. It can be separated from the latter by its shorter intestinal ceca which do not extend beyond the level of the testes as they do in *M. brachy-*

enteron. Furthermore, the vitellaria of *M. lanceatum* are confluent in the median line, a condition not found in *M. branchyenteron.*

Mesocoelium elongatum Goto and Ozaki, 1929
Plate III, Fig. 2

Diagnosis.—Body elongate, 1.78-1.82 long, 0.42-0.46 wide; anterior half of body spinous; oral sucker 0.2-0.25 in diameter, acetabulum, 0.17 in diameter, in anterior part of middle one-third of body; no prepharynx, pharynx 0.065 in diameter, esophagus 0.11 long; intestinal ceca short, only reaching anterior margins of testes; testes oval, 0.10-0.14 by 0.09-0.12, on each side of acetabulum and partially overlapping it; cirrus pouch large, 0.13 by 0.05; ovary, 0.10-0.11 in diameter, posterior to right testis; vitellaria lateral, along lengths of esophagus and intestinal ceca with few follicles overlying them; excretory vesicle Y-shape, bifurcating posterior to ovary. Eggs 0.04-0.043 by 0.025- 0.027.

Type host.—*Diemyctylus pyrrhogaster.*

Type localities.—Hiroshima, Sendai, Tokyo, Japan.[2]

Type specimen.—Not recorded.

Pearse (1932) and Yamaguti (1936) reported this species from the same host; Yamaguti reported it from Siga, Japan, while Pearse did not give the exact location in Japan. Yamaguti (*ibid.*) also reported *Mesocoelium elongatum* in *Rana rugosa* from Siga, Japan, and Ozaki (1936) reported it in *Geoemyda spengleri* from Loochow Island, Japan.

Mesocoelium elongatum most closely resembles *M. lanceatum,* however, it can be distinguished from the latter by its shorter intestinal ceca which are the shortest among all the members of the genus. The ceca do not even reach the level of the testes in *M. elongatum* while they do in *M. lanceatum.*

Mesocoelium monodi Dollfus, 1929
Plate I, Fig. 5

Diagnosis.—Body pear-shaped, wider at posterior end, averaging 3.0 long, 1.5 wide; cuticle completely spinous, more so in anterior half of body; oral sucker 0.34-0.37 in diameter, acetabulum 0.265 in diameter; short prepharynx, pharynx and short esophagus (0.125) present; intestinal ceca reaching anterior border of posterior one-third of body; testes rounded, 0.2-0.28 in diameter, on each side of acetabulum, partially overlapping it; cirrus pouch 0.21-0.24 by 0.08-0.1; genital pore at midlength of esophagus but to right of midline; ovary, 0.225-0.3, situated posterior to right testis; vitelline follicles of small and distinct units, lateral along the prepharynx, pharynx, esophagus and ceca; shape of excretory vesicle not observed. Eggs 0.035-0.038 by 0.02-0.023.

Type host.—*Chamaeleon gracilis.*

Type locality.—Souelaba, Cameron, North Africa.

Type specimen.—Museum of Natural History, Paris, France.

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[2] Goto and Ozaki (1929) reported *Mesocoelium elongatum* from the intestine of *Diemyctylus pyrrhogaster* collected at Hiroshima, Sendai and Tokyo, Japan, but did not indicate from which locality the type specimen was obtained, hence all three localities are listed as the "type localities."

Szidat (1932) reported *Mesocoelium monodi* in *Rana mascareniensis, Bufo regularis, Agama colonorium, Agama planiceps, Lygosoma fernandi,* and *Mabuia maculilabrus* from Liberia, Africa, and Baylis (1939) reported this species from *Chamaeleon etiennei* from the Valley of River Kwanga, Belgium Congo, Africa.

Mesocoelium monodi most closely resembles *M. crossophorum;* both species possess genital pores which are situated to the right of the median line. However, *M. monodi* can be separated from *M. crossophorum* by the lack of refractile spicules along its anterior sucker margins, and by its more medially placed testes which overlap the acetabulum dorsally.

Mesocoelium ovatum Goto and Ozaki, 1930
Plate III, Fig. 5

Diagnosis.—Body oval, 1.62-1.7 long, 0.62-0.65 wide; anterior half of body spinous; oral sucker 0.22-0.23 in diameter, acetabulum approximately 2/3 size of oral sucker; no prepharynx, pharynx 0.06 in diameter, and esophagus 0.045 long; intestinal ceca reaching beyond testes; testes oval, 0.15 by 0.11, anterior to acetabulum; cirrus pouch 0.09-0.12 by 0.06-0.08; ovary, 0.12-0.13 in diameter, behind right testis; vitelline follicles singularly follicular, main bodies of which are laterad to ceca with few follicles confluent in median line; excretory vesicle Y-shape. Eggs 0.038-0.04 by 0.024-0.026.

Type host.—*Rana rugosa.*
Type locality.—Sendai, Japan.
Type specimen.—Unknown.

Mesocoelium ovatum is probably most closely related to *M. minutum* and *M. japonicum.* It can be distinguished from *M. minutum* by its shorter intestinal ceca which extend only to the level of the anterior margin of the acetabulum and not beyond the acetabulum as in *M. minutum.* Furthermore, the ovary of *M. ovatum* is on the same level as the acetabulum while that of *M. minutum* is posterior to the acetabulum; the vitelline follicles of *M. ovatum* are few in number, with a few follicles from each side intermingling along the medial line; in *M. minutum* the follicles are numerous and are limited to the two lateral fields; finally, the body dimensions of *M. ovatum* (1.62-1.7 by 0.62 - 0.65 mm) are approximately three times as large as those of *M. minutum* (0.554 - 1.159 by 0.26 - 0.398 mm).

M. ovatum can be distinguished from *M. japonicum* by its fewer vitelline follicles; the shorter intestinal ceca which do not extend beyond the level of the acetabulum as in *M. japonicum;* by its body length (1.62 - 1.7 mm) which is considerably shorter than that of *M. japonicum* (2.0 - 2.3 mm); by the position of its ovary which is on the same level as the acetabulum and not partially posterior to it as in *M. japonicum;* and by the spacial relationship of its testes which are not in contact with each other as in *M. japonicum,* but lie on each side and anterior to the acetabulum.

Mesocoelium japonicum Goto and Ozaki, 1930
Plate III, Fig. 6

Diagnosis.—Body elongate, 2.0-2.3 long, 0.85-0.95 wide; cuticle spinous in anterior half of body; oral sucker 0.24-0.28 in diameter, acetabulum 0.15-0.19 in diameter; no prepharynx, pharynx 0.055 in diameter, esophagus short; intestinal ceca reaching past ovary but terminating in anterior one-third of body; testes oval, 0.14-0.17 in greatest diameter, anterior to acetabulum, touching each other medially; cirrus pouch large, 0.2 by 0.9; ovary oval, 0.15-0.21 in greatest diameter, partially posterior to acetabulum behind left testis; vitelline follicles of irregularly shaped, laterally situated acini along lengths of esophagus and intestinal ceca, and with many follicles confluent medially; excretory vesicle Y-shape (?). Eggs 0.045-0.049 by 0.026-0.03.

Type host.—*Polypedates buergeri.*

Type locality.—Yasuhara, Japan.

Type specimen.—Unknown.

Goto and Ozaki (1930) also reported this species in *Pseudosalamandra stejnegeri* from Kyushu, Japan.

Mesocoelium japonicum is most similar to *M. minutum* but can be distinguished from the latter by the configuration of the vitellaria which are confluent medially, a condition not found in *M. minutum;* by its body dimensions (2.0 - 2.3 by 0.85 - 0.95 mm) which are 2 to 3 times greater than those of *M. minutum* (0.554 - 1.159 by 0.26 - 0.308 mm); and by the relative sizes of the testes which in *M. japonicum* are smaller than the acetabulum and which in *M. minutum* are as large or larger than the acetabulum.

Mesocoelium americanum Harwood, 1932
Plate IV, Fig. 1

Diagnosis.—Body elongate, 1.2-2 long, 0.5-0.7 wide; cuticle spinous in cephalic region; oral sucker 0.21-0.27 in diameter, acetabulum 0.13-0.2 in diameter, esophagus short, never longer than pharynx; intestinal ceca extending to anterior margin of posterior one-third of body; testes irregularly oval, 0.07-0.14 by 0.105-0.15, partially anterior to acetabulum; length of cirrus pouch subequal to diameter of acetabulum; genital pore midway between cecal bifurcation and pharynx, to left of midline; ovary, 0.084-0.14 by 0.092-0.18, posterior to acetabulum and behind left testis; vitellaria lateral, of unequal-sized follicles, extending beyond cecal tips; excretory vesicle I-shape. Eggs 0.02-0.031 by 0.038-0.044.

Type host.—*Storeria dekayi.*[3]

Type locality.—Houston, Texas.

Type specimen.—USNM Helminth Coll. No. *30868;* paratype Coll. No. *30869.*

The type and paratype specimens were studied. *Mesocoelium americanum* is most similar to *M. japonicum* and *M. minutum*, however,

[3] Harwood (1932) recorded *M. americanum* from three hosts, *Storeria dekayi, Leiolopisma laterale* and *Eumeces fasciatus,* but did not specify from which of these the type specimen was recovered. The type specimen, however, is marked to have been recovered from *Storeria dekayi.*

it can be distinguished from these species by its longer intestinal ceca which extend to the anterior margin of the posterior one-third of the body; by the presence of a conspicuous prepharynx; and by the position of its genital pore which is lateral and to the right of the midline in the area of the esophagus. In *M. japonicum* and *M. minutum* the genital pore lies between the ceca, a short distance posterior to the cecal bifurcation.

Mesocoelium burti Fernando, 1933
Plate V, Fig. 2

Diagnosis.—Body elongate, 0.98-1.06 long, 0.45-0.53 wide; cuticle spinous; oral sucker averaging 0.175 in diameter, acetabulum, averaging 0.131 in diameter, posterior to and adjacent to cecal bifurcation; no prepharynx, pharynx 0.06 in diameter, esophagus extremely short; intestinal ceca extending posterior to midlength of body; testes rounded, averaging 0.14-0.122, immediately posterior to acetabulum, left one slightly anterior to right; cirrus pouch short, partially overlapping acetabulum; ovary oval, 0.152 by 0.078, posterior to left testis; vitelline follicles uniform in size, lateral in position, extending to cecal tips; excretory vesicle Y-shape, extending anteriorly to level of cecal tips. Eggs 0.035-0.036 by 0.019-0.022.

Type host.— *Rhacophorus maculatus.*
Type locality.—Colombo, Ceylon.
Type specimen.—British Museum of Natural History.

Pereira and Cuocolo (1940) postulated that *M. burti* represents the young of *M. marrsi* and hence considered the former synonymous with *M. marrsi.* This postulation was made without evidence from life history studies of either species and these workers did not indicate that they had examined young specimens of *M. marrsi.* Morphologically the two species can be separated by the relative size and position of their gonads. In *M. marrsi* the testes are on the same level as the acetabulum and their diameters approximate that of the acetabulum; in *M. burti* the testes are posterior to the acetabulum. Furthermore, the acetabulum of *M. burti* is in the intercecal space immediately posterior to the cecal bifurcation while that of *M. marrsi* is more posteriorly located. The specimens of both species as described by Fernando (1933) contained eggs in their uteri. Since the members of *Mesocoelium* are known not to be progenetic, it must be assumed that the specimens are all mature, hence the writer considers *M. burti* and *M. marrsi* as distinct species.

The similarity of *M. burti* to *M. incognitum, M. mesembrinum, M. oligoon, M. geoemydae* and *M. magrebense* is approximately equal and it can be distinguished from these species by its comparatively short and wide cirrus pouch, and by the position of its acetabulum which lies anteriorly in the intracecal space, touching the medial margins of the ceca and the posterior margin of the cecal bifurcation, a condition not found in any other species of *Mesocoelium.*

Mesocoelium marrsi Fernando, 1933
Plate I, Fig. 6

Diagnosis.—Body irregularly oval, 0.52 long, 0.312 wide; cuticle aspinous; oral sucker averaging 0.148 by 0.131; acetabulum in middle of body, 0.105 in diameter; prepharynx short, pharynx 0.061 in diameter, esophagus extremely short; intestinal ceca reaching posterior one-third of body; testes globular, 0.098-0.113 by 0.073-0.087, left testis in middle of body, overlapping acetabulum, right testis overlapping cecum and touching its mate; cirrus pouch small, approximately one-third the diameter of testes in length; ovary, 0.105 by 0.078, posterior to but in contact with right testis; all vitelline follicles of subequal dimensions, extending along lengths of ceca between and lateral to them; excretory vesicle Y-shape with the point of bifurcation lying anterior to level of cecal tips. Eggs few, limited to posterior one-third of body, averaging 0.035 by 0.022.

Type host.—*Rhacophorus eques.*

Type locality.—Ohiyu, Ceylon.

Type specimen.—British Museum of Natural History.

Mesocoelium marrsi most closely resembles *M. monodi*, however, it can be separated from the latter by its body length which is approximately one-sixth as long as that of *M. monodi*, by its less extensive vitellaria, and by its medially situated genital pore.

Mesocoelium danforthi Hoffman, 1935
Plate II, Fig. 1

Diagnosis.—Body elongate, 1.31-1.65 long, 0.54-0.58 wide; cuticle aspinous; oral sucker 0.296-0.3 by 0.328-0.336, acetabulum 0.148-0.172 in diameter; prepharynx present but indistinct, pharynx 0.11 by 0.085, esophagus extremely short, absent in some; intestinal ceca reaching past middle of body; testes, 0.104-0.108 by 0.072-0.076, obliquely lateral to acetabulum; cirrus pouch averaging 0.146 long; ovary subspherical, 0.1-0.136 by 0.08-0.096, larger than testes, behind and sometimes contiguous with right testis; vitelline follicles comparatively sparse, from level of oral sucker to below cecal tips; excretory vesicle Y-shape. Eggs small and numerous, 0.032-0.036 by 0.019-0.02.

Type host.—*Celestrus pleii.*

Type locality.—El Yungue, Puerto Rico.

Type specimen.—USNM Helminth Coll. No. *39570.*

The type specimen was studied. *Mesocoelium danforthi* most closely resembles *M. crossophorum* but can be distinguished from the latter by the absence of refractile spicules along the margins of its oral sucker, by the position of its genital pore which is medial instead of lateral as in *M. crossophorum.*

Mesocoelium geoemydae Ozaki, 1935
Plate V, Fig. 3

Diagnosis.—Body elongate, wider anteriorly than posteriorly, 1.55-1.85 long, 0.54-0.55 wide; cuticle spinous; oral sucker 0.22-0.25 in diameter, acetabulum 0.1-0.12 in diameter; prepharynx short, pharynx 0.08 in diameter; length

of esophagus slightly more than 1.5 times the diameter of acetabulum; intestinal ceca reaching middle of body; testes, 0.14-0.2 in greatest diameter, irregularly shaped, posterior to acetabulum; cirrus pouch 0.15 by 0.07; ovary oval, 0.08-0.13 in diameter; vitelline follicles lateral, extending from midlength of esophagus to ends of ceca; excretory vesicle Y-shape, the cornual bifurcation at level of cecal ends. Eggs 0.045-0.048 by 0.027-0.03.

Type host.—*Geoemyda spengleri.*

Type locality.—Loochoo Island, Japan.

Type specimen.—Unknown.

Mesocoelium geoemydae most closely resembles *M. oligoon* and *M. incognitum*, however, it can be separated from the former by its equal-lengthed intestinal ceca since the ceca of *M. oligoon* are not of equal length; and from the latter by the characteristics mentioned earlier in the consideration of *M. incognitum.*

Ozaki (1935) reported the flame-cell pattern of *M. geoemydae* to be 2 [(3+3+3)+(3+3+3)] which is identical with that described in *M. sociale* by Sewell (1920), in *Brachycoelium trituri* by Byrd (1937), in *Margeana californiensis* by Cort (1919), and in *Glypthelmins rugocaudata* by Yahata (1934). This information adds further evidence to the author's contention that the genus *Mesocoelium* is closely related to *Brachycoelium, Margeana* and *Glypthelmins.*

Mesocoelium leiperi Bhalerao, 1936
Plate II, Fig. 2

Diagnosis.—Body elongate, 1.97 long, 0.825 wide; cuticle spinous; oral sucker 0.24 by 0.225, acetabulum 0.18 in diameter; no prepharynx, pharynx 0.065 in diameter, esophagus extremely short, 0.03 long; intestinal ceca reaching posterior boundary of middle one-third of body; testes oval, 0.113-0.123 in greatest diameter, on each side of acetabulum and partially overlapping it; cirrus sac 0.095 by 0.035; genital pore on midline, posterior to cecal bifurcation; ovary subspherical, 0.13 in greatest diameter, posterior to right testis, partially overlapping acetabulum; vitellaria of singular follicles, lateral, from level of anterior oral sucker to ends of intestinal ceca; excretory vesicle I-shape (?). Eggs 0.038-0.04 by 0.025-0.027.

Type host.—*Tropidonotus* (= *Natrix*) *piscator.*

Type locality.—Rangoon, Burma.

Type specimen.—Unknown.

Zerecero (1950) reported *Mesocoelium leiperi* in *Eumeces* sp. from Cuicatlan, Oaxaca, Mexico. This species most closely resembles *M. microon* and *M. schwetzi;* the body dimensions of the three species are within the same range. *M. leiperi,* however, can be distinguished from *M. microon* by its shorter esophagus, its longer intestinal ceca which extend to the posterior one-third of the body rather than to its midlength as in *M. microon,* and by its smaller cirrus sac the length of which is approximately one-half the diameter of the acetabulum, while that of *M. microon* is one and one-half times the diameter of the acetabulum. The diameters of the acetabula in both species are identical (± 0.18 mm).

M. leiperi can be separated from *M. schwetzi* by its longer intes-

tinal ceca and the absence of the typical large flask-shaped cirrus sac as found in *M. schwetzi.*

Mesocoelium minutum Park, 1939
Plate IV, Fig. 2

Diagnosis.—Body oval, 0.554-1.159 long, 0.26-0.398 wide; cuticle spinous; oral sucker 0.125-0.185 by 0.095-0.182, acetabulum 0.087-0.126 by 0.09-0.12; prepharynx present, pharynx 0.042-0.076 by 0.05-0.073, esophagus 0.042-0.095 long; intestinal ceca terminate posterior to ovary near midlength of body; testes oval, partially anterior to acetabulum, 0.07-0.168 by 0.07-0.162; length of cirrus pouch approximately three-fourths the diameter of acetabulum; genital pore medial, immediately posterior to cecal bifurcation; ovary, 0.064-0.154 by 0.07-0.145, posterior to right testis and below level of acetabulum; vitellaria of compact individual follicles, lateral to and along lengths of ceca; excretory vesicle Y-shape with cornual bifurcation below ends of ceca. Eggs 0.042-0.062 by 0.019-0.034.

Type host.—*Bufo vulgaris japonicus.*

Type locality.—Niwagun, Aichiken, Japan.

Type specimen.—Helminth. Coll., Keizyo (Imperial) University, Keizyo, Tyosen, Japan.

Three specimens from Japan were examined. *Mesocoelium minutum* is most similar to *M. japonicum,* but can be distinguished from the latter by the characteristics given previously in the consideration of *M. japonicum.*

Mesocoelium travassosi Pereira and Cuocolo, 1940
Plate II, Fig. 3

Diagnosis.—Body oval, 2.67-3.11 long, 1.25-1.36 wide; cuticle spinous in anterior half of body; oral sucker 0.3-0.32 in diameter; acetabulum in anterior one-third of body, diameter of 0.2-0.24; prepharynx absent, pharynx present, inconspicuous esophagus if any; intestinal ceca extending posterior to midlength of body; ovary, 0.25-0.29 by 0.21-0.26, posterior to right testis; testes irregularly shaped, 0.25-0.3 by 0.18-0.23, situated on each side of acetabulum; cirrus pouch, 0.2 by 0.1-0.12; genital pore at point of cecal bifurcation; male and female gonads in anterior one-third of body; vitellaria of large irregularly shaped follicles, lateral to ceca, from lateral boundaries of oral sucker to near ends of ceca; excretory vesicle Y-shape (?). Eggs 0.033-0.037 by 0.025-0.026.

Type host.—*Bufo* sp.

Type locality.—Paraiba, Brazil.

Type specimen.—Not recorded.

Two specimens from San Paulo, Brazil, were studied. *Mesocoelium travassosi* most closely resembles the generotype, *M. sociale,* however, it can be distinguished from the latter by its shorter intestinal ceca which only extend to the middle of the body while the ceca of *M. sociale* extend to the posterior one-third of the body; furthermore, the vitelline follicles of *M. travassosi* are extremely irregular in outline and are less extensive than those found in *M. sociale.*

Mesocoelium crossophorum Pérez, 1942
Plate II, Fig. 5

Diagnosis.—Body oval, 1-1.1 long, 0.4-0.5 wide; cuticle completely spinous; oral sucker 0.6-0.175 in diameter with prolonged digit-like cuticular projections along anterior and lateral margins (10-12 anteriorly, 6 along each lateral margin); acetabulum 0.13 in diameter; prepharynx present, pharynx 0.065 in diameter, esophagus extremely short; intestinal ceca reaching slightly posterior to ovary; testes oval, averaging 0.11 by 0.08, on each side of acetabulum; cirrus pouch large, length approximates greatest diameter of testes; genital pore to right of midline, lateral to esophagus; ovary rounded, 0.115 in diameter; vitelline glands independently follicular, extending from oral sucker to beyond ends of ceca and are lateral to ceca; excretory vesicle Y-shape. Eggs 0.08 by 0.065.

Type host.—*Bufo peltacephalus.*

Type locality.—Jamaica, Cuba.

Type specimen.—Unknown.

Mesocoelium crossophorum is the sole species of the genus which possesses refractile spicules along the margins of its oral sucker. The phylogenetic significance of these projections is unknown and their presence in only this species of the Brachycoeliidae is hardly sufficient evidence to postulate that the Brachycoeliidae is closely related to the Echinostomidae. Rather, the author considers *M. crossophorum* a specialized member of the genus *Mesocoelium* characterized by the presence of the refractile spicules which are independent in origin from the spines of the echinostomes.

Mesocoelium sibynomorphi Ruiz and Leão, 1943
Plate III, Fig. 3

Diagnosis.—Body elongate, 3.7-4.7 long, 1.4-1.7 wide; cuticle aspinous; oral sucker 0.325-0.331 in diameter; acetabulum 0.282-0.339 in diameter, both suckers in anterior one-third of body; prepharynx present, pharynx with diameter of 0.127-0.141, esophagus of medium length; intestinal ceca short, barely extending beyond level of ovary, in anterior half of body; testes irregularly oval, 0.268-0.339 by 0.197-0.268, on each side of acetabulum, left one slightly more anterior; length of cirrus pouch approximates diameter of acetabulum; ovary 0.212-0.367 by 0.226-0.268, posterior to left testis, below acetabulum; vitellaria of small independently follicular masses limited to areas lateral to ceca from oral sucker to ends of ceca; excretory vesicle Y-shape, cornual bifurcation posterior to cecal tips. Eggs 0.036-0.039 by 0.022-0.026.

Type host.—*Sibynomorphus m. mikanii.*

Type locality.—Coronel Pacheca, Brazil.

Type specimen.—Not recorded.

Three specimens from San Paulo, Brazil, were studied. *Mesocoelium sibynomorphi* most closely resembles *M. brachyenteron*, however, it can be distinguished from the latter by the position of its genital pore which is on the midline, anterior to the cecal bifurcation, and not posterior to the bifurcation as is found in *M. brachyenteron;* by the position of the vitellaria which are more anterior, extending from the lateral margins of the oral sucker posteriorly to the level of the

testes and not along the lengths of the ceca beyond their tips as found in *M. brachyenteron.*

Mesocoelium mesocoelium (Cohn, 1903) n. comb.
Plate II, Fig. 4

Syns. *Haploderma mesocoelium* Cohn, 1903.
Pintnaria mesocoelium Poche, 1907.
Mesocoelium schwetzi Dollfus, 1950.

Diagnosis.—Body oval with pointed anterior and tapering posterior ends; 0.98-1.65 long, 0.325-0.66 wide; cuticle spinous in anterior half of body; oral sucker 0.183-0.248 by 0.169-0.232; acetabulum 0.127-0.161 in diameter; prepharynx not seen, pharynx 0.08-0.098, esophagus extremely short (0.01); intestinal ceca reaching posterior to midlength of body; testes with diameters which approximate that of acetabulum, on each side of acetabulum; left testis slightly more anterior; cirrus pouch flask-shaped; ovary larger than testes, posterior to right testis and touching it; vitellaria of single irregularly shaped follicles, lateral to ceca, from lateral borders of oral sucker to ends of ceca; excretory vesicle Y-shape (?). Eggs 0.034-0.037 by 0.022-0.024.

Type hosts.—*Bufo regularis, Rana mascareniensis.*

Type localities.—Stanleyville, Belgium Congo, Africa; Bukama, Belgium Congo, Africa.[4]

Mesocoelium mesocoelium is the only species of the genus which possesses a flask-shaped cirrus pouch. Morphologically it most closely resembles *M. leiperi* but can be easily distinguished from the latter by its shorter intestinal ceca which extend only to the middle of the body and not to the posterior one-third as in *M. leiperi,* and by the flask-shaped cirrus pouch.

The genus *Pintnaria* was erected by Poche (1907) to receive *Haploderma mesocoelium* Cohn, 1903, an intestinal parasite of the lizard, *Draco volans,* from Java. Poche observed that the name *Haploderma* was preoccupied and hence not available, and suggested *Pintnaria* as the new name. The similarity between *P. mesocoelium* and the members of *Mesocoelium* is so striking that Odhner (1910) suggested that the two genera might be considered identical. Cohn (1903) stated that his specimens greatly resembled the members of *Dicrocoelium* and placed it in the same group.

Cohn's (1903) description of *P. mesocoelium* is the only one in existence. Neither Poche (1907) nor subsequent authors (Hughes *et al.,* 1942) have amplified the description. Cohn was not specific in delimiting the generic characteristics and his drawings (pp. 35, 36) failed to reveal any striking difference between *Haploderma* (=*Pintnaria*) and *Mesocoelium.* Of the few generic characteristics given (p. 37) only that of the extent of the uterine coils, *i.e.,* "Uterus in the posterior half of body," differs from the condition found in the members of

[4] Dollfus (1950) reported this species from two hosts, *Bufo regularis* from Stanleyville, Belgium Congo, and *Rana mascareniensis* from Bukama, Belgium Congo, but did not specify from which host the type was obtained, hence both hosts and localities are listed.

Mesocoelium. The incomplete sketch of a worm mount *in toto* (p. 35), however, showed uterine coils which reach far into the anterior half of the body. The validity of the genus *Pintnaria* is indeed questionable.

The dimensions of the body and internal organs of *P. mesocoelium* are within the same range and almost identical with those of *Mesocoelium schwetzi,* and the arrangement of the internal organs of the two species are identical. The author agrees with Odhner (1910) that the genus *Pintnaria* should be considered a synonym of *Mesocoelium,* and using the older name, reduces *M. schwetzi* into synonymy with *M. mesocoelium.*

Mesocoelium maroccanum Dollfus, 1951
Plate II, Fig. 6

Diagnosis.—Body elongate; cuticle spinous, 2-2.28 long, 0.42-0.49 wide; oral sucker 0.19-0.22 in diameter, acetabulum 0.12-0.147 in diameter, esophagus of medium length (0.058-0.085); intestinal ceca extending beyond midlength of body; testes comparatively small, approximately one-fourth the size of acetabulum, on each side of acetabulum and partially overlapping it; cirrus pouch large, length equal to twice the diameter of acetabulum; genital pore to left of midline at level of cecal bifurcation; ovary small, same size as testes (0.08-0.09 in diameter), posterior to left testis; vitellaria of small independent follicles, lateral to ceca, from level of cecal bifurcation to beyond ends of ceca; excretory vesicle I-shape (?). Eggs 0.037-0.043 by 0.023-0.026.

Type host.—*Chaloides ocellatus.*

Type locality.—Rabat, Morocco.

Type specimen.—Not recorded

Mesocoelium maroccanum most closely resembles *M. meggitti;* both species possess a genital pore which is situated to the left of the midline of the body and lateral to the esophagus. The length of the cirrus pouch of *M. maroccanum,* however, is twice the diameter of the acetabulum, while that of *M. meggitti* is equal to the diameter of the acetabulum. Furthermore, the testes of *M. meggitti* are elongate oval with diameters approximating the diameter of the acetabulum; the testes of *M. maroccanum* are only one-fourth the diameter of the acetabulum.

Mesocoelium georgesblanci Dollfus, 1954

Diagnosis.—Body elongate, 1.3-1.91 long, 0.46-0.58 wide; cuticle spinous in anterior half of body; oral sucker 0.236-0.242 in diameter; acetabulum 0.142-0.16 by 0.087; prepharynx present, pharynx 0.073-0.078 in diameter, length of esophagus subequal to diameter of acetabulum; testes oval, 0.083-0.113 by 0.13, immediately posterior to acetabulum, partially overlapping it along posterior margin; cirrus pouch large, length approximates diameter of acetabulum; genital pore median, at point of cecal bifurcation; ovary 0.075-0.085 by 0.1, posterior to left testis; vitellaria of small irregularly shaped follicles lateral to and extending from level of cecal bifurcation to ends of ceca; excretory vesicle I-shape (?). Eggs 0.023-0.027 by 0.0275-0.041.

Type host.—*Coelopeltis monsoessulana, Ipse legi.*[5]
Type locality.—Temara, North Africa.
Type specimen.—Not recorded.

Mesocoelium georgesblanci most closely resembles *M. megaloon* but it can be distinguished from the latter by the diameter of the acetabulum which is 0.14 - 0.16 in *M. georgesblanci* and 0.065 in *M. megaloon;* by the size of the testes which are 0.082 - 0.113 by 0.13 in *M. georgesblanci* and 0.181 by 0.129 in *M. megaloon;* by the position of the testes, completely medial to the ceca in *M. georgesblanci* and overlapping the ceca in *M. megaloon;* and by the vitelline follicles, smaller and situated along the entire lengths of the ceca in *M. georgesblanci,* but only along the anterior two-thirds of the cecal length in *M. megaloon.*

Mesocoelium magrebense Dollfus, 1954
Plate V, Fig. 5

Diagnosis.—Body elongate, 2.4 long, 0.66 wide; cuticle spinous; oral sucker 0.267 in diameter; acetabulum 0.1 by 0.075, no prepharynx reported, pharynx 0.1 by 0.075, length of esophagus approximately three-fourths diameter of acetabulum; intestinal ceca reaching midlength of body; right testis, 0.125 by 0.125, on same level as acetabulum; left testis, 0.145 by 0.125, posterior to acetabulum; ovary posterior to right testis, 0.17 by 0.16; cirrus pouch approximately two-thirds the diameter of acetabulum; vitellaria of singular irregularly shaped follicles extending from level of pharynx to cecal ends; excretory vesicle Y-shape. Eggs 0.025-0.028 by 0.029-0.042.
Type host.—*Zamenis hippocrepis.*
Type locality.—Tnine, Imi N'Nlit, North Africa.
Type specimen.—Not recorded.

Dollfus (1954) described this species from only one specimen. The species most closely resembles *M. burti,* but can be distinguished from the latter by the position of its acetabulum which is slightly more posteriorly placed and not adjacent to the intestinal bifurcation as in *M. burti.* In body size, *M. magrebense* is approximately two and a half times as long as *M. burti.* The ovary of *M. magrebense* is located to the right and on the same level as the left testis while in *M. burti* the ovary is on the same side but posterior to the left testis.

Mesocoelium brachyenteron Dollfus, 1954
Plate III, Fig. 4

Diagnosis.—Body oval, 3.3-4.8 long, 1.7 wide; cuticle spinous; oral sucker 0.379-0.34 by 0.33-0.381 in diameter; acetabulum 0.3-0.35 by 0.25-0.33; prepharynx present, pharynx 0.13-0.149 in diameter, length of esophagus subequal to diameter of acetabulum; intestinal ceca not reaching midlength of body;

[5] Dollfus (1954) did not clarify from which one of the two hosts the type specimen was obtained, hence both are listed.

testes 0.29-0.3 in diameter, right one on same level as left one, and left one posterior to acetabulum; cirrus pouch approximately as long as diameter of acetabulum; genital pore at point of cecal bifurcation; vitellaria consisting of individual follicles extending from level of cecal bifurcation posteriorly beyond ends of ceca; excretory vesicle Y-shape. Eggs 0.035-0.044 by 0.021-0.028.

Type host.—*Vipera lebetina.*

Type locality.—Rabat, Morocco.

Type specimen.—Not recorded.

Mesocoelium brachyenteron most closely resembles *M. sibynomorphi,* but can be distinguished from the latter by the differences previously cited in the discussion of *M. sibynomorphi.*

DISCUSSION

Because of the great morphological similarities between the species of *Mesocoelium,* the author postulates that they are monophyletic in origin. The above revision of the genus and the annotated list of recognized species are based on the morphology of adult forms. Except for the life history of *M. lanceatum* (=*M. brevicaecum*) as reported by Ochi (1930) no other life history is known within this genus; it is suspected that further contributions in life cycle studies will reduce other species into synonymy.

The following key to the species of *Mesocoelium* has been constructed using specific characteristics which the author feels are of sufficient consistency to be of value.

KEY TO THE GENUS MESOCOELIUM

1. Testes at level of acetabulum.
    2. Intestinal ceca extending beyond midlevel of body.
        3. Genital pore median, anterior to intestinal bifurcation.
            4. Testes overlap ceca .... *sociale* (Lühe, 1901)
            4. Testes not overlapping ceca.
                5. Vitellaria of minute independent follicles .... *microon* Nicoll, 1914
                5. Vitellaria of large fused follicles .... *carli* André, 1915
        3. Genital pore median, posterior to intestinal bifurcation.
            6. Cirrus pouch length approximately one-half diameter of acetabulum .... *leiperi* Bhalerao, 1936
            6. Cirrus pouch flask-shaped, its length subequal to diameter of acetabulum .... *mesocoelium* (Cohn, 1903), n. comb.
        3. Genital pore median, at level of intestinal bifurcation.
            7. Diameters of testes subequal to that of acetabulum, left testis completely overlaps acetabulum .... *marrsi* Fernando, 1933
            7. Diameters of testes shorter than that of acetabulum, vitellaria of small singular follicles .... *danforthi* Hoffman, 1935
            7. Diameters of testes greater than that of acetabulum, vitellaria of irregular, partially fused follicles .... *travassosi* Pereira and Cuocolo, 1940
        3. Genital pore lateral to midline, anterior to intestinal bifurcation.
            8. Genital pore on left of esophagus.

9. Length of cirrus pouch subequal to diameter of acetabulum ....*meggitti* Bhalerao, 1927
9. Length of cirrus pouch approximately twice diameter of acetabulum ....*maroccanum* Dollfus, 1951
8. Genital pore on right of esophagus.
10. With refractile spicules along borders of oral sucker ....*crossophorum* Pérez, 1942
10. Without refractile spicules along borders of oral sucker ....*monodi* Dollfus, 1929
2. Intestinal ceca terminating in anterior half of body.
11. Vitellaria confluent in median line.
12. Intestinal ceca reaching level of testes ....*lanceatum* Goto and Ozaki, 1929
12. Intestinal ceca not reaching level of testes ....*elongatum* Goto and Ozaki, 1929
11. Vitellaria not confluent medially.
13. Genital pore anterior to intestinal bifurcation ....*sibynomorphi* Ruiz and Leão, 1943
13. Genital pore posterior to intestinal bifurcation ....*brachyenteron* Dollfus, 1954
1. Testes situated anterior to level of acetabulum.
14. Intestinal ceca terminating in posterior half of body.
15. Genital pore on right of midline, anterior to intestinal bifurcation ....*americanum* Harwood, 1932
15. Genital pore on midline, posterior to intestinal bifurcation ....*minutum* Park, 1939
14. Intestinal ceca terminating in anterior half of body.
16. Testes contiguous ....*japonicum* Goto and Ozaki, 1930
16. Testes not contiguous ....*ovatum* Goto and Ozaki, 1930
1. Testes situated posterior to level of acetabulum.
17. Intestinal ceca terminating in anterior half of body.
18. Ovary smaller than testes ....*geoemydae* Ozaki, 1935
18. Ovary larger than testes ....*magrebense* Dollfus, 1954
17. Intestinal ceca terminating in posterior half of body.
19. Genital pore at point of cecal bifurcation.
20. Intestinal ceca of unequal length ....*oligoon* Johnston, 1912
20. Intestinal ceca not of unequal length.
21. Length of cirrus pouch subequal to diameter of acetabulum ....*mesembrinum* Johnston, 1912
21. Length of cirrus pouch longer than diameter of acetabulum ....*georgesblanci* Dollfus, 1954
21. Length of cirrus pouch shorter than diameter of acetabulum.
22. Diameter of testes smaller than that of acetabulum ....*incognitum* Travassos, 1921
22. Diameter of testes subequal to that of acetabulum ....*burti* Fernando, 1933
19. Genital pore anterior to cecal bifurcation ....*megaloon* Johnston, 1912

It is apparent from the listing of type hosts and the other records for the species of *Mesocoelium* that the members of this genus parasitize both amphibians and reptiles in which they are found in the small intestines.

The geographic distribution of *Mesocoelium* appears to be some-

what cosmopolitan, however, most of the species have been described and reported from the Far East, Australia, and South America. No species of *Mesocoelium* have ever been reported from Europe and Dawes (1946), in his monograph of the trematodes of Great Britain and continental Europe, did not record the presence of this genus in those areas. A study of the ranges of the species has not been attempted since the information available is so inadequate.

SUMMARY

The genus *Mesocoelium* Odhner, 1911 is reviewed and 28 species are recognized as valid. The diagnostic characteristics of the valid species are considered. *M. waltoni* Pereira and Cuocolo, 1940 is considered synonymous with *M. incognitum* Travassos, 1921; and *M. brevicaecum* Ochi, 1930 and *M. pearsei* Goto and Ozaki, 1930 are both considered synonymous with *M. lanceatum* Goto and Ozaki, 1929.

Pintnaria mesocoelium Poche, 1907 is considered synonymous with *Mesocoelium schwetzi* Dollfus, 1950, however, the older name *mesocoelium* is adopted in accordance with the rules of nomenclature, hence *M. mesocoelium* (Cohn, 1903) n. comb.

A key to the species of *Mesocoelium* is given.

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Inter- and Intrahabitat Movements of the Rough-Skinned Newt, *Taricha torosa granulosa* (Skilton)

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Qualitative data obtained by direct observation is the usual basis for conclusions on various aspects of amphibian life history. The present study involves a technique whereby a temporary pond was fenced and traps were used to study the activities of various species of amphibians. This method enabled maintenance of a record of passage into and out of the pond and correlation of these travels with environmental factors. Some of these quantitative field data plus laboratory and conventional field techniques are here applied to give a more complete picture of certain non-reproductive aspects of the life history of a western North American salamander, *Taricha torosa granulosa* (Skilton). These observations are related in their reference to movements of these newts.

Although this paper is limited to life history considerations, mention of nomenclature used seems appropriate. Recent taxonomic treatments of the genus *Taricha* (Riemer, 1958; Pimentel, 1958) show differences of opinion regarding the relationship of *torosa* and *granulosa,* i.e., are they species, or subspecies of a single species? In addition, Riemer gave good reasons for assigning two previously described subspecies, *simulans* and *twittyi,* to the synonomy of *granulosa.* This seems to be the only possible conclusion from Riemer's work. Elimination of these two races removes the last major problem, distribution pattern, from my interpretation of the relationships. I believe two species of *Taricha* now exist, *T. rivularis* and *T. torosa. T. torosa* is represented by two groups of closely related subspecies, the *torosa* group with *torosa* and *sierrae,* and the *granulosa* group with *granulosa* and *mazamae.*

The general patterns of the life histories of the two species of western North American *Taricha* are known (Chandler, 1918; Miller and Robbins, 1954; Riemer, 1958; Ritter, 1897; Smith, 1941; Stebbins, 1951; Storer, 1925; and Twitty, 1942). *Taricha* behavior does not differ greatly from that of other newts of the family Salamandridae. Part of the year is spent on land and the remainder in water. Land existence is assumed to be a time of subterranean quiescence. Aquatic life is associated with reproductive activity and larval growth. Eggs are laid in water and hatch into aquatic larval stages. The larvae metamorphose and become terrestrial. These immature animals remain on land until they attain sexual maturity. At the next breeding period, the new, as well as old, adults move to water. After adults complete reproduction they again assume an underground life. A

frequently mentioned condition in newt life history is the marked morphological difference between land and aquatic males. Most of the differences are associated with either the presence of skin turgidity in aquatic males, or its absence in terrestrial males. In *Taricha* males the turgid appearance is allied with marked reduction in dorsal coloration, smooth rather than rugose skin, and increased tail length and tail fin height.

Only a few of the present topics have received critical attention in the past. Many individuals have described the aquatic habitat of *Taricha,* but only the already cited works of Riemer, Stebbins and Twitty give comparative treatment of the western North American newts. *T. rivularis* is a mountain brook form. In *T. torosa,* the *torosa* group inhabit both rapid moving and quiet water, but the *granulosa* group are mostly quiet water forms. It is also known that these newts display mass migrations to breeding ponds, but such movements are limited to females.

This study of *granulosa* outlines the kinds of aquatic habitats used and preferred, duration of aquatic existence, mechanisms involved in leaving and reaching ponds, sexual differences in the pattern of migration to ponds, differences in travel to temporary and permanent ponds, wanderings of aquatic newts, activity periods, sexual and habitat differences in leaving ponds, and terrestrial existence. These life history data are related in that all aspects have some bearing on movements of these salamanders.

Acknowledgments.—I am indebted to a number of individuals for assistance during this investigation. For pertinent suggestions relative to the gonadal cycle and for the use of prepared microscopic slides showing seasonal variation in *granulosa* gonads, the writer is grateful to Dr. Ernst J. Dornfeld, Oregon State College. Special thanks are due Dr. Philip C. Dumas, College of Idaho, for making observations at Oak Creek pond when neither the author nor Dr. Robert M. Storm could accumulate data. I am indebted to Dr. Robert M. Storm, Oregon State College, for his help, advice, criticism and encouragement throughout the course of study and to Dr. Glenn A. Noble, Calif. State Polytechnic College, for reading the manuscript.

PROCEDURES AND RESULTS

Methods, although varied, were simple. Direct field observations were used in all phases of this study and extended from August, 1949, through June, 1952. These observations were made in western Oregon and northwestern California, but were concentrated in the vicinity of Corvallis, Benton Co., Oregon. Both permanent and temporary aquatic habitats were explored. The most frequently observed permanent pond was Peavy Arboretum pond, 7 miles north of Corvallis. This large, man-made body of water covered approximately 3 acres and had a maximum depth of about 25 feet. More observations were made here rather than in other permanent ponds because of the proximity of the pond to our laboratories and the large numbers of newts which

could be seen readily. The temporary pond most frequented for qualitative field observations was on a shelf of Coffin Butte, an area that also contained a permanent pond. Coffin Butte is about 15 miles north of Corvallis. The Butte pond was also used because of accessibility and number of newts visible.

Experiments were conducted in both the laboratory and the field to investigate the mechanisms of homing behavior to and from ponds and the characteristics of terrestrial life. A minimum of ten trials were used in all studies.

A fenced pond facilitated the gathering of quantitative data on movements in the field, gave insight into causes of these activities, and verified laboratory experiments. This temporary pond occurred next to Oak Creek on Oregon State College property.

Oak Creek Pond

The writer participated in the Oak Creek pond study during the first two aquatic periods, 1950-51 and 1951-52. In the 1950-51 season quantitative records were started after some newts were observed in the pond. Although construction began prior to winter rains, a fence was not completed until January 8, 1951, and the traps were first checked on January 9. Both sexes were observed in the pond prior to fencing. The first male was seen on December 9, and the first female, on December 29, 1950 In the 1951-52 season the fence was secure before the first newt migrated into the pond.

Details of project construction, etc., are given elsewhere (Storm and Pimentel, 1954). It seems sufficient here to state that the fence was made of 1/4-inch hardware cloth and was ten inches high. Also, the 14x6x5 inches traps were formed of bronze window screen. Screen funnels at each end of the traps allowed newts to enter but appeared to prevent their exit. In the present paper the study area is described in some detail for the first time, and *Taricha* data are summarized and correlated with environmental factors. Also, observation methods and difficulties, as they apply to the rough-skinned newt, are treated here with greater emphasis than in the general paper.

Description of Area.—The pond, located in a pasture, is surrounded by herbacious vegetation which is kept close-cropped by cattle. The pond and fence were protected from the cattle by a barbed-wire fence (not shown on any figure). The word *fence* as used below refers to the amphibian barrier and not the barbed-wire structure. Areas labeled as vegetation consist mostly of willows (*Salix* sp.) and black cottonwoods (*Populus trichocarpa*). The location of the temporary stream entering the pond, its direction of flow, and the exiting stream into Oak Creek are diagramed (Fig. 1). Similar features are shown for Oak Creek.

The pond had a surface area, when full, of approximately one-seventh acre. The water depth varied with the rate of flow of the

entrance stream. When the stream stopped, the depth was approximately 3.8 feet. Much greater water depths, shown as peaks in Figures 3 and 4, were the result of debris accumulating on the fence across the outlet stream and causing this fence to act as a partial dam to the flow of water.

Numbered stakes were placed around the margin of the pond at ten-foot intervals (Fig. 2). These reference points aided in pin-pointing observations and were also used to designate individual traps. The number assigned to each trap was taken from the stake closest to a direct line from the trap to the pond. The only exception to this was for the inner and outer traps between stakes 42 and 43. These traps are referred to as inside and outside No. 42.5.

The fence worked as a barrier to most organisms entering and leaving the pond. The only known exceptions were some large adult rainbow trout (*Salmo gairdnerii*) that readily jumped over the fences. The barrier caused animals approaching the pond to drift into traps. Traps were placed to indicate direction of approach of the forms entering or leaving. The precision with which individual traps indicated direction of approach was dependent upon how effective each trap was in catching newts. Effectiveness was measured by the check traps (Nos. 2, 41, 43 and 64) placed closest to the traps on the inlet and outlet of the pond (Fig. 2). It is not believed that these check traps would capture many newts unless adjacent traps were ineffective. Newts entering by a landward route would probably not contact the limited area covered by the check traps. Animals entering via the stream would be caught only if the traps placed along the stream edge did not function. Because the check traps caught very few in-

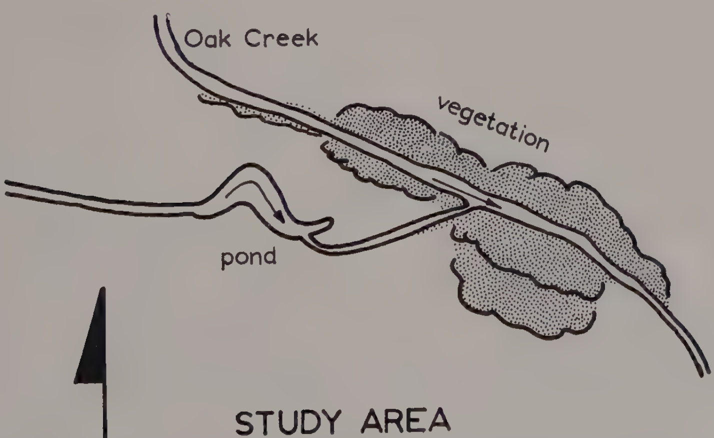

Fig. 1.—General area of study. Of special significance is the location of the study pond and vegetation along Oak Creek. Arrows indicate the direction of water flow in the study pond and in the creek.

dividuals (Figs. 5 and 6), the capture method is believed to be very effective in indicating direction of approach to the fence.

Observation Methods.—Observations were usually made daily but more frequent visits did take place. The following data were recorded for each newt: number, sex, size (if other than average), anomalies, exact point of observation, breeding condition of females (gravid or non-gravid), and degree of skin turgidity of males. In addition water level and temperature (taken at about 6″ depth) were recorded. The taking of water temperatures at different levels was considered, but soon rejected, because the influx of water and shallowness of the pond led to uniform temperature throughout the depths. All of these data except size and anomalies are used in this paper.

Maximum value of observations necessitated accurate identification of individual newts. Toe-clipping was used from the start but with little hope that it would prove satisfactory. The literature at that time would have one believe that salamanders would regenerate these structures too rapidly for mutilation to be of much value. Gordon (1952) and Stebbins (1954) have since shown that this method is entirely satisfactory for certain plethodontid salamanders. For the present study toes and portions of the metacarpals were removed by deep V-shaped cuts. When animals with regenerating toes were encountered the code number was recut. This method was effective because animals marked during the first season were readily recognized the second season.

Amphibians of the study pond showed different rates and degrees

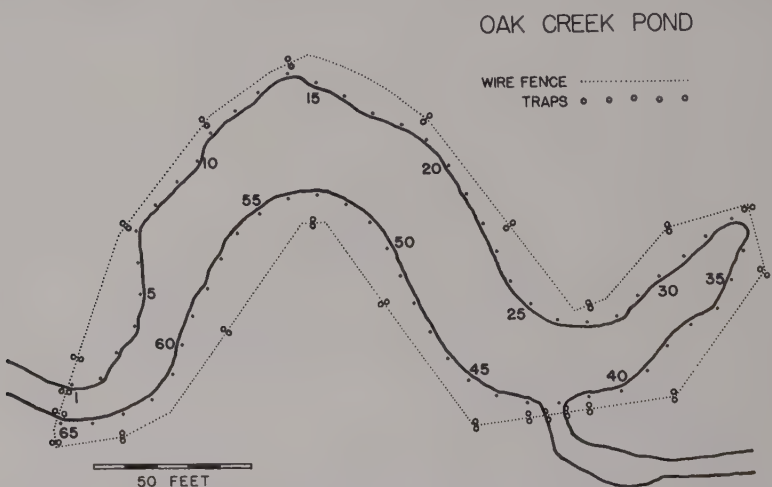

Fig. 2.—Oak Creek pond and details of project. Dotted line indicates a ten-inch high hardware cloth fence, circles indicate the position of traps, and dots indicate reference stakes placed at ten-foot intervals. Every fifth stake is numbered in the figure. Direction of water flow is from left to right.

of toe regeneration. Marking of the northern red-legged frog (*Rana a. aurora*) was most effective. Amputation in this form is believed to result in permanent loss of digits, because recaptures, including those of a year later, showed no visible regeneration. Both rough-skinned newts and Pacific tree frogs (*Hyla regilla*) were effectively numbered, but some toe replacement did occur. A gray blastema soon formed at the amputation sites in both animals. The blastema either developed into small, sometimes anomalous, lighter colored digits, or simply healed without any regeneration taking place. Toe replacement in the long-toed salamander (*Ambystoma macrodactylum*) was rapid and regenerated toes often were similar to the originals. Moreover, different toes on the same animal tended to show different rates and degrees of replacement. For this reason, it is doubtful if the recognized recaptures of the following season were assigned their proper number. It is even possible that growth could obscure markings during a single aquatic period in this ambystomid salamander. A single Pacific giant salamander (*Dicamptodon ensatus*) was trapped, but it was not recaptured.

Because of a belief that toe-clipping would prove unsatisfactory, numbered metal tags were also tried. The smallest and apparently the best of those available was a type of fingerling tag (Style 1005, Size 1,

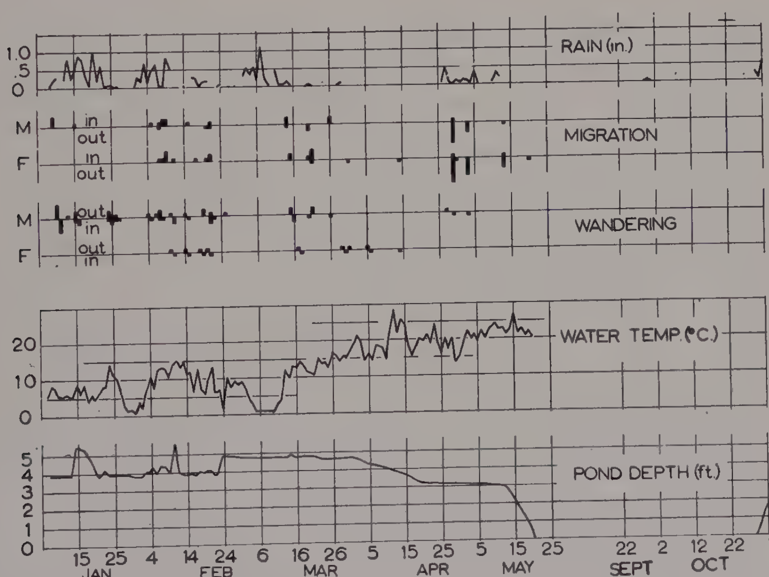

Fig. 3. Pond Data, 1950-51.—From top to bottom are graphed daily rainfall in inches; date of first entrance and final exit, males on the line above that for females; wandering, with the sexes separated as for migration; water temperature in degrees centigrade; and pond depth in feet.

National Band and Tag Co., Newport, Ky.) It was hoped that these tags could be clamped on lower jaws as was the practice with certain frogs. Laboratory newts showed immediate lower mandible ulceration around the tag. Tags placed in the fleshy portion of the base of the dorsal fin of lab newts appeared to produce no adverse reaction. However, when tags were placed on study pond newts, the fins ulcerated and the tags dropped from the tail within a few days. These tagged salamanders could always be identified later, not only by their clipped toes, but also by deformities and lighter coloration in the healed area at the base of the tail.

Difficulties.—Certain factors may have affected the data, but they are believed to have no bearing on the conclusions derived from this study. These difficulties were undermining of entrance and exit fences, the source of rainfall data, water temperature and depth, and different observers.

Breaking down of the barriers at sites of water entrance and exit occurred during periods of high water. Although it was thought that undermining could result in the loss of much data on newt movements, such was not the case. The lack of difficulty is attributed to marked reduction of newt movement at times of flood. All field observations indicate that newt activity is extremely limited on such occasions. Moreover, interpolation of data often alleviated the problem caused by unrecorded movement. Interpolation was possible when two entrances, or exits, occurred two days apart. For example, records of exit two days apart without an intervening entrance would necessitate such an entrance beneath the fence. Only three wanderings of the 1950-51 season and one of the 1951-52 season did not have the necessary prior data to pinpoint time of exit. In these cases newts last recorded inside the pond but captured outside were assumed to have been absent only one day. On this basis a "guessed time of movement" was interpolated and recorded in Figures 3 and 4 and Tables I and II. In these few cases the interpolated path, i.e., trap, was assumed to be at the same location as the last trap used, but the opposite member of the pair. For example, if an animal last recorded inside the pond entered by outside trap No. 1, it was assumed that the animal left the pond the day before via inside trap No. 1. Because no guessed movement was the only activity recorded for a particular day, it is believed that this embellishment of data does not affect the general conclusions of this paper. The purpose of interpolation of data is to give a complete picture of travel in and around the pond. It is possible, however, that entrances, wandering and exits occurred and were not recorded; but it is not believed that they took place to a significant extent.

Rainfall data were not from the area of the pond but from the Oregon State College weather station. Because the station is less than one-fourth mile from the pond and observations at both points never produced observable differences in rainfall, the data were assumed

fairly accurate. Moreover, the quantitative aspects of rainfall were not indicated to be of great significance in newt behavior. The presence or absence of ground moisture, however, is of significance. Therefore, these data from some distance are believed valid for the purposes for which they are used.

The pond was visited every day and all newt movements were recorded for the proper day. However, on certain occasions, when no newts were in traps, water temperature and sometimes water depth were not recorded. Such occasions amounted to fewer than twenty days in each season. For these days water depth is assumed and water temperature interpolated from minimum-maximum air temperatures of the weather station. This also is not believed to affect conclusions because water depth always was recorded when it was other than "near average" and weather data estimations were found to be reliable approximations of recorded water temperature. Moreover, no constant temperature recording devices were available and all temperatures, except those for maximum temperature of the second year are merely temperature of the water sometime during the day. There is an additional interpolation of environmental data; the observations from August 28, to November 17, 1951 (Figs. 3 and 4), are based on a very few recordings.

The procedures in obtaining data were of such a nature that little bias could be involved due to different observers. Storm and I usually made the daily visits together but on a few occasions only one of us checked the pond. For a short time, March 18-22, 1951, when both of us were gone, Dumas made daily records. Prior to this time Dumas became thoroughly familiar with procedures. It seems unlikely that personal bias could have resulted from the techniques of any of us.

Movements of Marked Newts.—Some confusion can result in discussion of movements because this subject is considered in different ways. First, all movements have some relationship to the time of year, i.e., a period in the annual cycle of the animal. Second, there is the type of movement itself. Finally, the mechanisms and stimuli which result in a particular movement are considered. In general, *Taricha* movements are fairly well known. From June to November, prior to the breeding season, most newts are subterranean. Upon assuming a surface existence in the latter part of the year, they spend a short time in seemingly non-oriented travel. This is referred to as either sporadic movement or the sporadic period. The brief sporadic period is terminated by breeding migration. Breeding migration is not likely to cause time of year-, type of movement-confusion because the phenomenon is well known, directional and limited to a small portion of the annual cycle. Finally, after completion of reproductive activities, postreproductive migration to underground retreats takes place. This activity is, of course, limited to a short time in an individual's annual cycle and is well known. All of these kinds and periods of movements are emphasized by the data from marked newts of the study pond.

Results.—Marking newts at Oak Creek pond disclosed a previously unreported movement made by breeding newts. During the reproductive period and prior to final exit from the pond, marked individuals were recorded leaving and then returning to the pond. In many individuals this behavior occurred many times. This movement is called wandering. The term *wandering* describes the appearance of the activity to the observer. The stimuli and behavior patterns producing the phenomenon are not known. The first movement into a pond, breeding migration, and last movement out of a pond, post-reproductive migration, are not considered part of wandering.

Wandering in the above sense was displayed by twelve males and eight females in the 1950-51 season and fifteen males and ten females in the 1951-52 season. Table I indicates the more significant wanderings of individuals during the two seasons. The columns of the table denote season, i.e., 1950-51 or 1951-52; sex of the single newt involved; and movement data. The movement data include date of movement and trap of exit or entrance (abbreviated). An exit trap is designated by an asterisk; an entrance trap has no such designation. For example, an animal leaving by trap number 65 on December 31, would be recorded 12/31, No. 65*. An animal entering via trap number 65 on the same day would be recorded 12/31, No. 65. Individual wanderings are bracketed.

Much of the behavior classified as wandering at the study pond

TABLE I.—Representative wandering data

Season	Sex	Date and path of exit or entrance
1950-51	♂	(1/10, No. 65*—1/11, No. 1) (2/10, No 65*—2/11, No. 63)
	♂	(1/10, No. 65*—1/11, No. 1) (1/26, No. 65*—1/27, No. 1)
	♂	(1/24, No. 65*—1/25, No. 7) (2/4, No. 42*—2/5, No. 41)
	♀	(2/10, No. 34*—2/11, No. 34) (2/18, No. 65*—2/19, No. 1) (2/20, No. 65*—2/21, No. 1)
	♀	(2/14, No. 42*—2/15, No. 43)
	♀	(4/5, No. 65*—4/16, No. 1)
1951-52	♂	(12/21, No. 65*—12/23, No. 65) (1/12, No. 65*—1/13, No. 1) (1/27, No. 1*—1/28, No. 1) (2/3, No. 2*—2/14, No. 14) (2/16, No. 42*—2/25, No. 42.5) (4/28, No. 27*—4/29, No. 34)
	♂	(1/31, No. 62*—3/23, No. 42.5)
	♂	(2/1, No. 14*—2/27, No. 14)
	♂	(2/1, No. 34*—2/3, No. 33) (2/24, No. 42.5*—2/25, No. 42.5) (3/3, No. 1*—3/7, No. 63) (4/30, No. 41*—5/1, No. 42)
	♂	(4/19, No. 34*—4/20, No. 34)
	♀	(1/31, No. 44*—2/1, No. 43) (5/6, No. 18*—5/12, No. 14) (5/13, No. 14*—5/20, No. 14)
	♀	(2/3, No. 33*—2/4, No. 34) (4/8, No. 65*—4/9, No. 1)
	♀	(2/13, No. 65*—2/14, No. 1) (2/15, No. 65*—2/16, No. 1) (3/3, No. 65*—3/5, No. 1)
	♀	(5/6, No. 18*—5/20, No. 34)

* Designates exit trap.

may have been merely activity within an aquatic environment, because exits through aquatic traps followed by re-entrance by the same water route were classified as wandering. Although such movements are of some consequence, there is a great deal of true wandering (Table I).

Table II emphasizes pathways of movement during the two annual cycles. Here the number of individuals that existed and entered via each trap are totaled. Figures 3 and 4 graph, from top to bottom, amount of daily rainfall; dates of first entrance (above the line) and final exit (below the line), first for males and then for females; wandering (exit above and re-entrance below the line), first for males, then for females; water temperature; and depth of water in the pond.

TABLE II.—Summarization of movement data

	1950-51 Period								1951-52 Period							
Trap	Entrance		Wandering				Exit		Entrance		Wandering				Exit	
			Out		In						Out		In			
No.	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1	6	2	..	..	19	3	..	..	5	3	2	1	9	4	1	..
2	..	..	..	..	..	..	..	..	..	2	1	..	..	..	..	..
7	1	..	..	..	1	..	..	..	1	3	..	..	..	..	..	..
11	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
14	..	1	..	1	..	1	4	3	..	3	3	1	3	2	12	5
18	2	..	..	..	..	..	..	2	1	6	..	3	..	1	1	2
23	..	..	..	..	..	..	..	..	2	3	..	..	..	..	4	2
27	..	..	..	..	..	..	..	..	2	5	1	..	..	..	..	3
32	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
33	1	3	..	..	..	..	..	2	..	5	..	1	1	1	3	..
34	1	..	1	1	1	1	7	11	1	2	4	1	3	1	7	10
39	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
41	..	2	..	..	1	..	..	1	1	..	1	..	..	..	1	3
42	6	6	3	2	3	1	2	1	5	3	3	3	3	1	1	1
42.5	..	..	..	..	..	..	..	..	7	8	3	1	4	2	..	1
43	..	..	..	..	..	1	..	..	1	1	..	..	..	..	..	..
44	..	..	..	..	..	2	..	..	..	..	..	1	..	..	..	..
53	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..
59	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..
63	..	..	..	..	1	..	..	..	..	..	1	..	..	..	..	..
64	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
65	..	..	22	5	..	..	3	1	2	4	5	3	1	2	2	..
Total	17	15	26	9	26	9	16	21	29	49	25	15	24	14	32	30
Were in?	31	20							17	8						
Stayed							29	10							14	25
Died							2	4								2
Total	47	35					47	35	46	57					46	57
Total Wanderers			12	8							15	10				

Figure 3 shows all environmental records starting on January 7, 1951. Newt data starts on January 9, and all information are continuous until May 20, 1951, when the pond dried up. After a gap of time, all environmental and animal observations are again recorded from September 22, to November 1, 1951. No salamanders were seen or trapped during this latter period.

Figure 4 data are complete from November 2, 1951, to May 20, 1952. The pond dried on May 20 in both years. Maximum water temperature recordings were added to Figure 4 for a short period of time, April 16, to May 20, 1952.

The two sets of pond recordings are considered to be roughly equivalent. Very slight variation does exist in water temperature and rainfall but not to the degree necessary to explain other seeming deviations. Less water depth fluctuation took place during the second season but this was not due to any environmental factor. Relatively stable water depth was the result of an upstream screen placed to catch floating debris before it could block the entrance fence. No data peculiarities can be attributed either to the screen or to reduced water fluctuation. Inconsistencies in wandering and migration, especially first entrance into the pond, can be attributed to incompleteness of the 1950-51 observations. The greater number of newts in 1951-52 would seem to account for any unexplained seasonal differences.

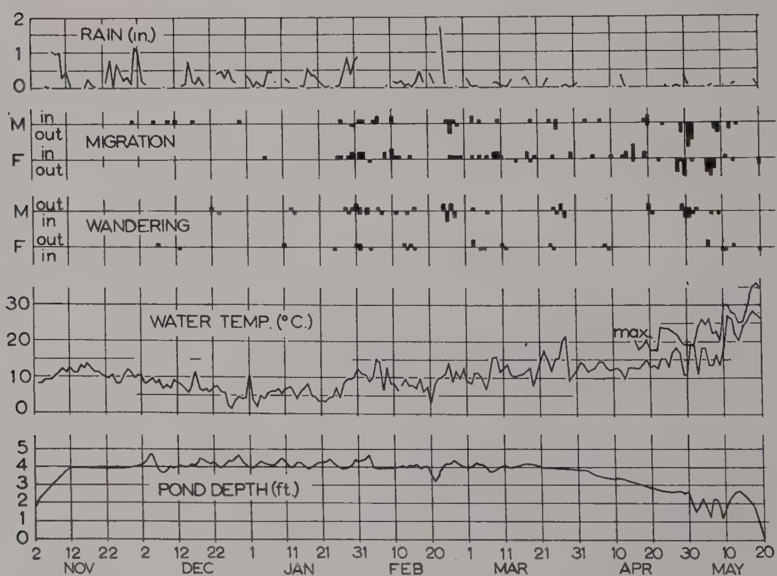

Fig. 4. Pond Data, 1951-52.—Data presented as in Figure 3. Maximum daily recorded water temperature is added for a short period in April and May.

Correlations—Various associations between newt movements and environmental factors are shown in Figures 3 and 4. Most travel occurred during periods of rainfall. Low water or air temperature are related to reduced newt activity. The lowest temperature at which movement occurred was near 5°C. High water temperature and lowering water level were associated with permanent exits from the pond. The figures indicate sexual differences in amount of activity and periods of entrance and exit.

EXPERIMENTS

In addition to study pond investigations, experiments were conducted from June, 1951, to June, 1952. The experiments were a normal outgrowth of the accumulation of data. Observations were recorded on 6x8-inch cards and filed according to a life history outline based on Fitch (1949). Reference to this file at any time showed where additional information was needed. Limited records in certain categories of the outline were the reason for various experimental studies.

Observations on the behavior of newts moving on land suggested the importance of the senses of sight and smell. Czeloth (1931) came to a similar conclusion in his work on European newts of the genus *Triturus*. Czeloth's methods were simplified and other procedures were added. Results indicate that any pond exit and entrance is accomplished by the senses. The pond data have a bearing on these laboratory results.

POSTREPRODUCTIVE MIGRATION

Pond Data.—Postreproductive migration entails movement from a pond to the autumn retreat. The concentrated areas of permanent exit indicated in Table II can be visualized by observing Figures 1, 2 and 5.

Early final departures from the study pond were aquatic. These individuals may have "lost the pond" rather than actually left as the result of innate behavior or a response to environmental conditions. This is believed to be the case because males were of the aquatic morphological phase, females were gravid, and the activity of those remaining would belie any environmental stimulus causing final exit.

Later final departures were via land traps, and are believed to be either physiological or environmental responses. The possibility of a physiological response was indicated by the newts' essentially land form. These departures occurred after the temporary stream into Oak Creek dried. They were toward, and concentrated at, the nearest dark horizon, i.e., vegetation along Oak Creek (Figs. 1 and 5).

Experimental Results.—The visual reaction to a dark horizon could be established in the laboratory. A circle, about 30 feet in circumfer-

ence and one foot high, was made of white and black paper placed on edge. This formed a ring of insignificant width and an artificial horizon about one foot high. Paper was arranged into 5 three feet wide white artificial horizons alternated with 5 three feet wide black artificial horizons. Newts believed to be making permanent exits from Peavy Arboretum pond were used for this study. Individual animals were placed under a box in the center of the ring. When the animals seemed to have quieted from previous handling the box was removed. Of 10 males and 10 females used, under ideal conditions, all repeatedly crawled toward dark (black paper) rather than light (white paper) interruptions of the horizon. The probability of either sex displaying such behavior due to chance alone is 1 in 1024. If one considers the lack of sexual difference in behavior and combines the results, the probability becomes 1 in the square of 1024. Field data also tend to establish the seeking of dark horizons as the mechanism newts use to find land habitats.

Attempts to establish the sense of smell as a factor in finding an autumn retreat were inconclusive. In the laboratory, when visual and humidity stimuli are excluded, the odor of earth causes newts to gather even if they are unable to come into direct contact with the earth. Also, under like circumstances, animals separated by a simple maze often congregate. This is believed to be an olfactory rather than a humidity response because the maze was lined with wet paper towels. In

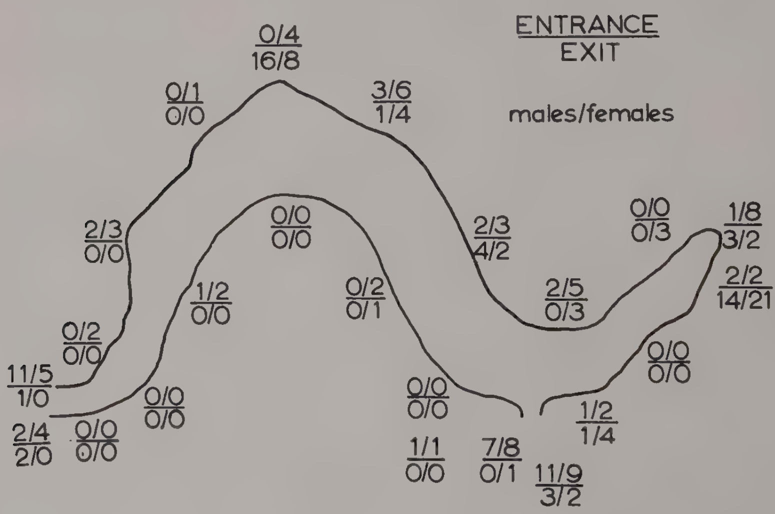

Fig. 5.—Avenues of migration to and from pond. The sexes are separated as a fraction, ♂/♀. Pondward migrations are indicated above the horizontal lines and landward migration below these lines. The data represent the total observations for both seasons. Reference to Figure 1 shows that exits are concentrated toward dark horizons, i.e., vegetation.

addition to this possible odor detection of their kind, they may perceive the odor of a given locale. The peculiar odor of a favorable hiding place seems to be a stimulus which can serve as an orientation for finding the place again. Of course this may mean that they can perceive their own odor and be seeking that rather than any particular site. These olfactory responses will either not take place or be haphazard unless favorable air currents are present. The nature of the various responses cause the belief that the sense of smell, if of importance in final departure from ponds, is secondary to vision.

BREEDING MIGRATION

Pond Data.—Breeding migrations occur overland for various distances to the breeding ponds. The pathways of entrance are indicated in Table II. Figures 1, 2 and 5 show the position of entry traps and how they relate to the surrounding terrain. During the first season of Oak Creek pond study there was a preponderance of entrances via inlet and outlet streams, and in the second season there was an even higher proportion of such entries. The difference is thought to reflect the lost data of 1950-51. In both periods most aquatic approaches were upstream, but records are insufficient to assume any significance to this fact. Land approaches into the study

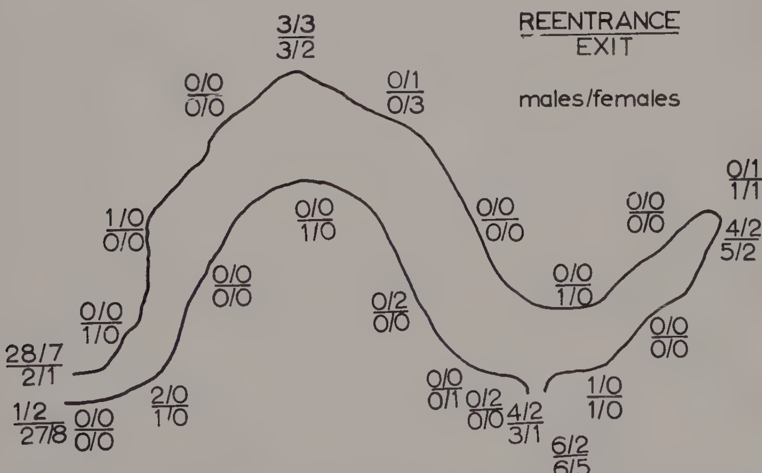

Fig. 6.—Avenues of wandering away from and back to the pond. The sexes are separated as a fraction, ♂/♀. Pathways of exit are indicated below the horizontal lines and re-entrance above these lines. The data represent the total observations for both seasons. Reference to Figures 1 and 5 show that wandering exits, like landward migrations, show concentration toward dark horizons, i.e., vegetation.

pond show some slight deviation from exit data; however, it is believed that most entrances reflect sites of subterranean life, hence indirectly direction of exit from the pond.

Stream orientation was considered as a factor in aquatic entrances. In Peavy Arboretum water flowed into the pond during periods of rainfall. This rill was along the main route of entrance. At Coffin Butte newts migrated uphill in runoff from the temporary pond. Patterns at other ponds showed some with upstream and others with downstream routes. Lack of facilities for laboratory consideration of this problem caused it to be abandoned.

Experimental Results.—Pond entrance studies were first started in the field. In these studies no association of entrance with either time of day, air or ground temperature, ground moisture, or amount of precipitation could be established. These field experiments tended to emphasize particular responses to stimuli. It was found that animals taken from the water return promptly from a distance of 3 meters. On a downhill bank the direct way to the water is immediately taken; on a level bank a preliminary wandering usually occurs before the right direction is assumed. Slightly greater delay occurs when an uphill bank is involved. Animals placed on level ground 10 meters from a pond show much variation in reactions. A few will immediately head for the pond, some will wander with seeming lack of orientation, others will seek shelter under objects and some will wander farther from the pond. Repeated field experiments displayed no sexual differences in behavior. A "typical" trial involved 25 males. Of the males released 10 meters from the pond, 7 reached the pond within fifteen minutes, 10 more within one-half hour, two more within forty-five minutes, two went under bark, and four disappeared in the underbrush away from the pond. None of these data are considered to indicate normal time responses because of the observed effects due to experimental conditions. Also, the responses may have been modified due to my presence. Such studies, however, do aid in ascertaining mechanisms of entrance.

Possible environmental aids to entrance, suggested by preliminary studies, are downhill slopes, sight, odor and humidity. Animals taken from a body of water and released on land exhibit a strong tendency to travel downhill, but migrating animals already "oriented" toward the water are geotactically indifferent. In going to ponds vision is not necessary because blindfolded newts are seemingly as successful as controls. On the other hand, if the sense of smell is blocked proper orientation seems to be due to chance, so the reaction seems to be to odor or humidity. This thought led to further laboratory work. In experiments the newts moved with odor-free currents, but toward "desirable" odor currents. When other stimuli are removed they perceive and seek areas of highest humidity. If an air current is saturated with water vapor, movement for the most part is toward the source of the current; however, travel is often with the air current.

Therefore, olfactory stimuli appear to be more significant than humidity stimuli and the animals react to air current as follows: negatively to air currents without odorous substances, positively to air currents with odorous substances and usually positively to humid air currents.

TERRESTRIAL ACTIVITY

Pond Data.—This activity is considered to include that portion of the life history between permanent exit and the sporadic period prior to breeding migration. Some members of both sexes spent subterranean life within the confines of the study pond fence. Both sexes were seen entering cracks in the dry pond bed. Added weight is given the premise of pond site underground life by the newts first seen in Oak Creek pond each season. Males were first seen on December 9, 1950, and November 1, 1951; females on December 29, 1950, and December 5, 1951. The 1951 data show the presence of newts in the pond prior to any entrances. The 1950 data probably give the same information, but this cannot be assumed because the fencing was not completed at that time.

Experimental Results.—Lack of data on terrestrial activities again resulted in laboratory studies. Use was made of a 3x8-foot enclosure in which land and water conditions could be simulated. A 2x8-foot portion became a terrarium. This was filled with earth to a depth of about one foot. The dry aquarium was screened from the land; and five males and five females, found leaving Peavy Arboretum pond, were placed into the terrarium. The newts constructed six burrows to the bottom of the enclosure. Two burrows each contained two newts and one, three newts; the rest contained individual salamanders. One burrow had a male and a female, another two males, and the other one male and two females. It is not known if salamanders sharing burrows united to construct these underground retreats. These amphibians lived almost four months underground without food or moisture in addition to that of the August subsoil they would have found near their pond. At the end of three months, although no activity was noted, a quart of water was sprinkled, as evenly as possible, over the surface of the soil. At this time none of the burrows had visible surface openings. Within 24 hours after sprinkling two males came to the surface but they returned to their underground retreats within 48 hours. It is assumed that reduced moisture, perhaps lower humidity, caused a return to subterranean existence. At the end of three and one-half months the same sprinkling process caused all males and one female to come up. Once again no open burrows were visible. Upon return of the newts underground, two days after sprinkling, water was placed in the aquarium for the first time and the barrier to the aquarium was removed. No activity was noted. Four days after the aquarium was filled, the terrarium surface was sprinkled again. The next day all males and two females were in the water. Another female entered a week later and the fourth the next day. During the time

it took the last two females to enter, the surface of the ground was kept moist. It was later found that the fifth female had died in her burrow. Males upon reaching the surface showed no visible development toward the aquatic morphology.

Sprinkling experiments and field observations indicate that rainfall stimulates subterranean newts to assume surface activity. However, rainfall was noted to stimulate all kinds of movements. At the time of the earliest fall rains only sporadic movement is stimulated. However, later in the season, rainfall may be stimulating breeding migration, wandering, or postreproductive migration as well as sporadic movement.

Allied to the above was the burial of five males and five females for a six-month period. Each was placed in a separate five quart can, the can was filled with soil to within three inches of the top and the remainder was filled with damp leaf mold. Soil and leaf mold were obtained from an area believed to contain underground retreats and were believed to have been comparable to such substrate. The cans were stored in a room where the temperature remained near 60° F. All males and three females survived. Although sluggish and visibly dehydrated when removed from the containers, they soon became active and shortly after being placed in water insufficient to cover them, the desiccated appearance was lost. The survivors showed no visible ill effects from the experiment after regaining water. These observations are the basis for the belief that the primary subterranean hazard is water loss. Finally, the conditions of this experiment are believed to be more severe than those of the usual subterranean retreat. Therefore, newts in nature probably can spend longer inactive periods without any permanent ill effects.

The above results, if accepted in their entirety, present some difficulty. In nature, individuals entering breeding ponds show morphological indication of being reproductively active; but the sexually inactive, experimental animals entered the water when they could. Perhaps this atypical behavior was due to laboratory conditions. Unfortunately no close check was kept on possible experimental animal land-water movements and no attempt was made to determine how long the animals would remain in water. Because of laboratory limitations, this project was abandoned two weeks after the first individual was known to enter the aquarium.

Because autopsies of newts removed from experimental burial showed uniform gonadal quiescence, these salamanders probably would not have reproduced that year. This agrees with the work of Miller and Robbins, (1954) on *torosa*. Their paper seems to establish an every other year breeding period for that newt. Further evidence that *granulosa* tends to reproduce every other year is indicated by the paucity of 1950-51 newts returning to the study pond in the 1951-52 season. If this cycle exists and laboratory results are dependable, individuals not breeding in a given season come to the surface and form part of the sporatic period population. At least part of this

population is in an interim stage between underground and aquatic existences. The non-reproductive animals can be distinguished from the prereproductives by gonadal condition. The non-reproductives show gonadal quiescence and prereproductives considerable gonadal development.

DISCUSSION

Movements are of four types, sporadic, pond entrance, wandering and pond exit; and take place at various times in the reproductive cycle. Upon leaving their underground retreats, newts first exhibit a kind of sporadic, seemingly non-directional activity. This is terminated by a second type, directional migration to water. Next, and also appearing to be without orientation, is wandering, i.e., exit from and return to the breeding habitat. Although wandering is characterized by a sexual difference, the significance and cause of this phenomenon are not completely clear. The last kind of travel, final exit for the season, is directional and, like most of the above behavior patterns, can be related as to cause and effect.

These four types of behavior could be diagnosed in the field only at the study pond. Here it was demonstrated that morphology is an indication, however a poor one, of the different activities. Miller and Robbins (1954), using gonadal histology and field work, diagnosed all movements but wandering and established morphological correlations with these instinctive patterns. Observations on *granulosa* adults in Oak Creek pond resulted in finding the same morphological clues to activity as those found in *torosa*. Breeding characters in sporadic movers show slight to moderate development and in pondward migrators moderate to maximum development. Wanderers display the same range of aquatic form as migrators; however, wanderers generally appear more aquatic. Exiting newts tend to exhibit the land phase. Morphologicaly, the latter are similar to sporadic movers; but landward migration is almost always later in the year, shorter in duration, and directionally away from the aquatic habitat.

The sporatic period is primarily a time of limited and secretive action. Miller and Robbins (1954) believe *torosa* takes 6-8 weeks to complete this activity. *T.t. granulosa* also wanders on land prior to migration to a pond but direct evidence for its duration is limited. One male was found on land about 100 yards to the northwest of the study pond. Twenty-one days later this newt entered the pond. The animal was observed under the same board for fifteen consecutive days, it then left and six days later was taken in an entrance trap. During the three-week period, obvious increase in aquatic morphology was noted. This delay in entrance is assumed to be related to reproductive development. The 6-8 week duration of this period in *torosa* is a reasonable estimate for its length in *granulosa*.

A series of events take place during the sporatic period. Rainfall results in subterranean newts coming to the surface. They are visibly desiccated, but a short period, less than 24 hours in the laboratory, in

moist surroundings results in recovery. The transfer from a quiescent to an active life, or perhaps some environmental factor, results in development of the secondary sexual characteristics of the male and the ova in the female. During this time the salamanders are to a limited extent on the move. The travels give the appearance of aimless, nondirectional periods of foraging. Marked individuals that were recovered were found within 50 feet of the site of original encounter.

Final approaches to ponds are along definite "highways" rather than at random from all directions. This is believed to be the general case despite the lack of strongly oriented land travel into Oak Creek pond (Fig. 5) The apparently haphazard land entrances are probably associated with sites of autumn retreat. On the other hand, the large number of inlet and outlet entrances establish the streams as two pathways. Elsewhere, preferred entrance routes were noted. The primary source of newts entering Peavy Arboretum pond was from the southwest. A definite path about one-fourth mile long could be traced. The highway consisted of a portion of dirt road and a short but straight section through dense Pacific coast forest. The Coffin Butte approach was uphill along a dirt road and extended for approximately 200 yards. The latter distance seems to be about average for such routes. No other migration distance was traced as far as that at Peavy Arboretum.

Pond entrance involves at least four factors, rainfall, temperature, physiology and odors. Of possible secondary importance are humidity and slope of terrain. The triggering mechanism, starting pondward movements, is rainfall. Precipitation of this kind causes some individuals to move if temperatures are not low. However, even if temperature is optimum, the triggering mechanism will not function unless the newts are "physiologically set" for movement. It is assumed that instinctive behavior patterns associated with sexual development must progress to a certain stage before migration can take place. The final important factor effecting entrance is environmental odor. This stimulus enables animals responding to other factors to locate a pond. Two additional factors, humidity and slope, may be secondary in orienting these salamanders toward water.

Newt breeding migration is characterized by a sexual difference involving numbers of individuals found together and date of the activity. Males tend to migrate singly, females often in groups; and males migrate before females. There are no records for mass male movements to water in the genus *Taricha*. The pond influx of males is gradual and starts about a month before the first females enter. Entrance is associated with rainfall. Each subsequent rain brings additional males until sometime in November or December when the first females arrive. In contrast to lack of records of many males proceeding toward breeding grounds, there are definite reports of numerous females migrating pondward. In western Oregon such female activities were observed between the second week of January (1951) and third week of February (1952). However, not all female

movement of this kind is of the group type. Before and after such aggregations there are individual and small group migrations. The observed entrances of many females were associated with permanent ponds. In the study pond, as well as in other temporary ponds, there was little indication of coordinate female entrance. This may be due partly to fewer newts inhabiting temporary ponds which would result in fewer individuals being involved even if mass migrations occur. Final entrances show no differences, they consist of individuals of both sexes.

The rough-skinned newt is found in a wide variety of aquatic habitats. Temporary and permanent ponds, as well as lakes, are frequented the most; but streams are inhabited to some extent. Botanically sterile bodies of water are shunned, but almost any other quiet water may be occupied. Apparently suitable ponds, widely isolated from surrounding vegetation, do not have these amphibians. Although strongly alkaline waters might be avoided, *granulosa* is found in bogs of relatively low pH. Observations indicate that temperature places no strict limitation on sites, but that it does limit the duration of the aquatic period.

Wanderings from and return to impounded waters is fairly common. These seemingly aimless journeys are usually limited to short distances from the pond. At Oak Creek pond in 1950-51 this activity was recorded in 12 of the 47 males and 8 of the 35 females; in 1951-52, in 15 of the 46 males and 10 of the 57 females. These data do not indicate a statistically significant difference between the sexes as to numbers involved. At Peavy Arboretum pond, males, and to a lesser extent females, could be observed to leave the water, travel about ten feet away and return. Wanderings in the vicinity of the study pond, like those around permanent ponds, were concentrated in certain areas (Fig. 6). In fact all travel into and out of the ponds tended to be along the same routes (compare Figs. 5 and 6).

Duration of absence from the study pond during wandering was usually short. Because the traps were usually checked only once each day, the trapping system could force newts to remain out of the pond as much as 24 hours. Therefore, short land excursions, as observed in permanent ponds, could not be recorded. Males showed a stronger tendency to remain out of water than did females. Of the 1950-51 males staying out more than one day, three remained outside 2 days; two, 4 days; and one each 5, 6, 7, 9, 23, 39 and 45 days. Only three 1950-51 females remained out of the pond more than one day, two, 6 days and one 11 days. In the 1951-52 males, two remained outside 2 days; three, 4 days; and one each 9, 11, 13, 14, 26 and 51 days. In 1951-52 females, two remained outside 6 days; and one each 2, 4, 7 and 14 days. Some of this period of newt absence was associated with the onset of weather conditions unfavorable for movement. However, there is no known cause for the extensive absences of the five males.

Individual records of total wandering give additional information

on the characteristics of this phenomenon (Table I). When duration of exit was short there was a definite tendency to return through or very near the trap opposite the exit trap. When the duration was longer, return was some distance from the site of the exit trap.

Temporary terrestrial excursions from water are associated with certain environmental factors. Warm rains seem to produce marked movements of this kind around ponds, but the wanderers are not readily segregated from newts making first entrance. In the study pond wandering can be associated with rainfall and temperature. Rainfall, or at least moist surroundings, appears to be the most important factor. In addition no movement of any kind was recorded when water temperatures were below 5° C. Also, no land movement took place when air temperatures were approximately 5° C. or lower. If no rainfall occurred, movements were almost entirely confined to water. Exceptions resulted when the surrounding herbaceous vegetation was moist. These environmental associations are not unique for wandering. They are also correlated with other movements.

A puzzling side issue to the subject of this paper was the correlation of certain wanderings with newt morphology. Although on the average approximately 20 percent of the diagnostic characters of a group of *granulosa* are *torosa*-like in appearance (Pimentel, 1958), at times 90 percent of the characters of salamanders wandering near a pond were *torosa*-like. At other times all, or most, newts would be "typical" *granulosa*. No reason for this morphological association is evident.

Literature on activity periods of western *Taricha* emphasizes daylight hours. The degree of activity has been interpreted by the conspicuousness of the newts. In *granulosa* this varies according to season and habitat. As the aquatic period progresses there is first an increase and then a decrease in observability. This cycle is directly associated with courtship activities. The activity of newts also shows a difference between land and water inhabitors. Terrestrial movements are generally limited to night or overcast periods. This association may be due to humidity or other factors, e.g., it was noted that warm rains stimulate such movements. There were contradictory observations on within-pond newts. Most temporary and all permanent pond field notes show no significant difference in conspicuousness of newts during given 24 hour periods, however, in the study pond, more movement was visible at night. Despite the latter contradictory evidence the general pattern was for an equality of within-pond movement throughout the various periods of any day.

The length of aquatic existence has been neglected in previous studies. Records that exist usually do not differentiate between temporary and permanent waters. Streams are not considered here, or elsewhere in this paper, because none were found with sufficient newts to make observations reliable. In temporary ponds the extent of habitation is approximately five to seven months (December 9, 1950, to May 20, 1951, and November 1, 1951, to May 20, 1952, in the

study pond); and in permanent ponds, ten months or more. In Peavy Arboretum the last observed newt was seen on September 1, 1951, and the first entering newt on November 4, 1951, so these salamanders might have been absent fewer than 64 days. It is possible that such bodies of water are populated the year around; however, not by the same individuals.

In certain areas *granulosa* may be entirely aquatic. Certain investigators (Bishop, 1943; Farner and Kezer, 1953; and Riemer, 1958) found both sexes with vestiges of gills. Riemer found this condition in *granulosa*, the others in *mazamae*. Riemer logically interprets this as a partial tendency on the part of *granulosa* toward neoteny.

Factors related to newts leaving ponds are more numerous in temporary than in permanent aquatic environments. Evacuation of temporary situations may result from either a period of high water temperature or lowering of water level (Figs 3 and 4), but there seems to be some ability for newts to withstand these stimuli until rainfall occurs. Only temperature is likely to be of influence in permanent ponds. The impression was gained that onset of terrestrial phase morphology is hurried by increasing water temperature. Newts kept at room temperature assume the terrestrial phase much faster than newts kept at lower temperatures. Keeping males out of water also hurries the onset of the land phase. The relationship between physiology and exit is not clear. Miller and Robbins (1954) found that male California newts not only remained in water but retained the aquatic phase after regression of the gonads. This is also the case in the rough-skinned newt. Yet assumption of the terrestrial phase in male *granulosa* takes place prior to permanent departure from breeding sites. Also of possible bearing is the earlier departure of females. The situation can be summarized as follows: females depart when egg deposition is completed; many males also leave early and may be reflecting the completion of part of their physiological cycle; however, other males remain longer and stay until water temperature, other environmental changes, or in the case of temporary ponds, low water drives them to the land.

Duration of aquatic life in reflecting entrance and exit shows sexual as well as habitat differences. Males start to enter ponds before females, but final entrances show no sexual or apparent habitat distinction. In Peavy Arboretum pond the first male was observed on November 4; and the first female, on December 5, 1951. Although the study pond dates for first entrance are later, if one considers the newts that spent terrestrial life in the dry bed, the sexes become active at essentially the same time as the newts at the arboretum. In the study pond the remaining entrance activity is much the same for both sexes (Figs. 3 and 4). Conditions at other temporary, as well as at permanent ponds seemed the same. First exits show only sexual difference, males tend to leave before females. Final exits tend to display no sexual difference in temporary ponds, but males stay in permanent

ponds much longer than females. In Peavy Arboretum pond the last male was seen on September 1, and the last female on July 31, 1951. In the study pond the dates for the same year are May 14, for males and May 20, for females.

Sight and resultant movement toward dark horizons were already indicated as the means of finding underground retreats. Instinctive movement toward dark areas may result in locating more available underground habitats, but this conclusion is not readily reconciled with such things as the presence of open meadow mouse (*Microtus*) burrows on the way to permanent retreats. However, the areas producing dark horizons (woods, etc.,) tend to be more buffered against environmental extremes than are open situations. This will be considered in more detail later.

There is an inconsistency in the data proving that all newts do not leave temporary pond sites when ponds dry. In 1950-51 of the 82 Oak Creek pond inhabitants only 17 of the 47 males and 15 of the 35 females entered after the area was fenced. Although additional newts probably entered prior to fencing, some are believed to have spent their previous land period within the area of the fence. It can be seen (Table I) that twenty-nine 1950-51 males stayed inside the fence at the end of the first season, but only seventeen 1951-52 males first appeared within the confines of the fence. For females these figures are ten and eight. The explanation of this inconsistency does not involve the simple loss of records on a few individuals because none of the newts that were inside the fence at the start of the 1951-52 period bore markings from the previous year. It is believed that these second season newts are members of a population that did not breed in 1950-51. Surprisingly, the activity of non-reproductives was never recorded within the study pond. Perhaps *granulosa* non-reproductives differ from those of *torosa* by not leaving their underground retreats until they next reproduce, but laboratory studies would belie this premise. Although of interest the activity of non-reproductives must remain a side issue of this paper. Of primary consideration is the indication that *granulosa,* like *torosa,* breeds on alternate years despite the four exceptions to be given to this pattern.

Storer (1925:51) indicated the paucity of field information on terrestrial *torosa* by stating, "Were *torosus* to breed on land like the local Plethodont salamanders it would probably be much less common in collections." Terrestrial *granulosa* are as difficult to find as any land-inhabiting salamander in western Oregon. The apparent rarity of newts on land is explained by their strong tendencies toward subterranean life. The only time truly terrestrial newts are likely to be found on the surface of the ground is during fall rains. Of the newts encountered at such times some were partially buried under debris and others had soil encrustations. Whether these were sporadic period prereproductives, showing gonadal activity, or non-reproductives, showing gonadal inactivity, was not determined. However, these and

already mentioned observations indicate that most of the period out of water is spent underground.

In western Oregon underground retreats are usually within areas of coast forest. The typical substrate is within the burrowing capabilities displayed by laboratory newts. These forests have a deep layer of humus covering the earth, so the soil is likely to retain moisture longer and to exhibit less temperature changes than that in non-forested areas. Moreover, all forest factors tend to produce the maximum buffering against environmental extremes that is available in western Oregon. Therefore, behavior seems to result in newts reaching areas most likely to enable them to withstand long periods underground.

The field data on duration of land life are quantitative only in regard to temporary ponds. Four females of the 1950-51 period returned to the study pond in the 1951-52 season. Reproductive notes on these individuals indicate that all laid eggs both seasons. The durations of absence for these females were 238, 273, 275 and 283 days respectively, so they are exceptions to the general pattern of breeding only on alternate years. Most newts spend approximately 18 months on land between reproductive periods. There was no evidence to indicate that non-reproductives became aquatic on non-breeding years.

Although many attempts were made to determine the degree of activity in subterranean newts, only one group of these salamanders was found. Three males went under a large rock on Coffin Butte on May 4, 1952. Two to three weeks later the opening was sealed. On June 5, 1952, the rock was removed and the three males disclosed. Each reacted sluggishly to a stimulus, the taking of cloacal temperatures, but all were obviously in a semi-torpid state. This condition is surprising because both the cloacal and ground temperatures were 12° C. This body temperature is generally associated with normal activity and not quiescence. Although this is an isolated record it would indicate that quiescence occurs and is of an innate physiological nature.

Water loss probably is the environmental danger of most importance on land. This danger appears to be reflected in part by the physiology and ecology of these animals. Quiescence in animals is generally considered to retard dehydration as well as other physiological hazards. Also, the underground habitats are buffered against any extreme change in environmental conditions. Moreover, a dehydration hazard is consistent with the importance of rainfall in stimulating return to surface activity. In experimental burial the obvious hazard was also dehydration. Newts are known to leave ponds and go underground during periods of rainfall. If one considers the non-reproductive phase as physiologically and instinctively specialized to prevent water loss, the fact that rainfall sometimes is associated with pondward and other times landward movements causes no difficulty. The contradictory movements are related to two entirely different phases of the life history and likely different behavior patterns.

There has already been some indirect reference to distance newts travel from ponds to underground sites. Observations were insufficient to obtain quantitative estimates. However, any distance over one-fourth mile is probably exceptional. This is believed despite the fact that a male was found about one mile from any source of surface water. At Peavy Arboretum pond most newts entered the ground within an area 20-75 feet from the pond. It is believed that at least 90 percent of the newts go underground within 200 yards of most ponds.

Summary

This study of *Taricha torosa granulosa* consists of portions of the life history directly reflecting movements. It considers kinds of aquatic habitats used, duration of aquatic existence, mechanisms involved in leaving and reaching ponds, sexual and habitat differences in migration to and from ponds, wandering of aquatic newts, activity periods, and terrestrial existence. Also, reasons are given for the use of present nomenclature.

Data were obtained from direct observation, simple experimentation and studies at a fenced temporary pond. The latter give data previously unobtainable. Although morphology gives clues to types of movement taking place, only trapping data completely segregate these activities.

Pond entrance is not direct from underground retreats; perhaps six to eight weeks are spent on land. Because most newts breed only every other year, non-reproductives of the season may be involved in this period of sporatic activity. Rainfall stimulates assumption of surface life. After development of reproductives is complete, rainfall associated with favorable temperature stimulates their migration to breeding ponds. Breeding sites are found by the sense of smell; humidity perception and downhill slopes to ponds may be of some aid.

Male movement to ponds starts about a month prior to that of females and is solitary. Although females show like activity, mass migrations also occur. However, female mass migration was observed only in entrances to permanent ponds. The pondward travel of both sexes shows concentrations along certain routes or "highways" at most ponds. Final entrances are individual activities in both sexes.

Although this newt is found in a wide variety of aquatic situations it is more numerous in quiet water ponds and lakes than in streams. Vegetation-free bodies of water, as well as aquatic situations without nearby vegetation, are avoided. Normally occurring temperatures and acidities probably do not exclude them from otherwise acceptable habitats.

Land wanderings from water and back to water frequently take place and are probably stimulated by warm rains. Less than half the newts are involved. When exit is for a short time, the animals tend to move and return within the immediate area of exit; but when exit is longer, they may re-enter some distance from the site of departure.

Although a like percentage of each sex takes part in wandering, males exhibiting this behavior wander more frequently than the females. Excursions of this kind are usually of short distance and duration, especially in females; but males are known to stay out 23, 26, 39, 42 and 45 days. These activities are concentrated in the area around ponds where all land movements are most frequently encountered.

Activity in a pond appears to be equal throughout any 24 hour period; however, there is a seasonal increase in activity as the breeding period progresses and decrease as this period wanes.

The length of aquatic existence shows sexual and habitat variation. In certain localities adults of both sexes bear rudimentary gills and are probably permanently aquatic. Other males are found at least ten months in permanent ponds and about seven months in temporary ponds; females, approximately eight and six months in these habitats, respectively. Although males are observed a month longer than females in permanent ponds, temporary pond newts tend to show no sexual difference in exit dates. Departing newts have almost lost the aquatic phase morphology.

Newts leaving ponds early will use an aquatic route if it is available. However, newts that must leave ponds by a land route do so by means of vision. Seeking dark horizons is the primary mechanism for finding land retreats but the sense of smell may be of some aid. Only a tentative characterization of exit is possible. Females depart when egg deposition is completed. Many males also leave early and may be reflecting the completion of part of their physiological cycle. However, other males remain longer and stay until water temperature, other environmental changes, or in the case of temporary ponds, low water drives them to land. Not all newts leave temporary pond sites. Some enter an underground existence within the limits of the dry pond bed and most of these autumn retreats are within one-fourth mile of the breeding pond.

The underground period may be as little as three or four months for permanent pond newts. Temporary pond newts may frequently have to remain subterranean for seven months. Because most newts breed only every other year fossorial existence is usually 12 months longer. These newts can burrow to a limited extent.

The habit of seeking dark horizons for autumn retreats results in newts reaching wooded or similar areas providing optimum buffering from environmental extremes. The greatest danger to newts in these retreats seems to be dehydration. The salamanders probably assume a physiological state of quiescence while underground.

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Germination Studies of Aerial Bulblets of Allium vineale L. and A. canadense L.[1]

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This investigation was undertaken in an effort to determine under what conditions and circumstances the aerial bulblets of *Allium vineale* L. and *Allium canadense* L. would no longer be capable of germination. The problem arose because of the incidence of these bulblets, particularly *A. vineale,* as impurities in grain crops, such as wheat and barley.

The specific problem was the question of legal definition of the term "noxious weed seed" as applied to the bulblets in state and federal seed laws. These laws generally assumed *Allium* bulblets to be capable of germination under all conditions. A number of seed companies had questioned the validity of the application of the laws without exception to situations in which the companies felt the bulblets could no longer be considered viable.

Materials

The major portion of this work was devoted to *Allium vineale;* the larger size of the aerial bulblets of *Allium canadense,* and its less frequent distribution, make it less of a pest.

The material used in the work with *Allium vineale* was collected from 1943 to 1951 inclusive, from states along the Atlantic coast, and as far west as Ohio. Only a few samples of *Allium canadense* were available when the experiments began, limiting the work with these bulblets until the summer of 1951, when a number were collected in the vicinity of Ithaca, New York. Gross differences in the two species are shown in Figure 1.

A minimum of two replications of 100 bulblets each was used for each lot tested, with three or more replications in some experiments. All bulblets were stored at room temperatures unless otherwise noted.

Procedures and Results

determination of standard temperature and medium

The first step was the determination of a standard temperature and germination medium which would result in the maximum possible germination. *Allium vineale* was used in the determinations.

The mean germination percentage of all lots germinated at 68°F.

[1] A portion of a thesis submitted for the Doctor of Philosophy degree, Cornell University, 1952, under guidance of Dr. W. C. Muenscher.

was significantly higher than those germinated at 86°F. At the higher temperature the appearance and growth rate of various fungi was more rapid than at the lower temperature. Thus, the former was used during the course of the experiments.

The selection of a germination medium was considered with possible alternatives of the paper-towelling-germinator method, or the seed-flat, greenhouse method used by Justice and Whitehead (1942).

Two sets of two replications of eight lots of bulblets were used. One set was germinated between paper towelling, the other was planted about one-half inch below the surface of a mixture of equal parts

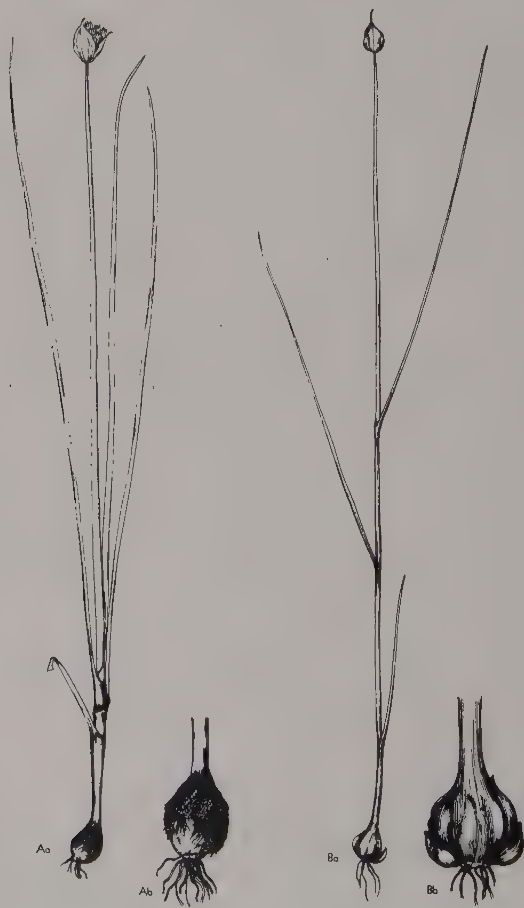

Fig. 1.—Gross distinguishing features between (A) wild onion (*Allium canadense*) and (B) wild garlic (*Allium vineale*). (Aa, Ba — habit sketches detailing origin of leaves; Ab, Bb — nature of the bulb.)

of sand, peat and soil, in seed-flats, and set in a greenhouse at a temperature of approximately 72-75°F. The results obtained at the end of a ten-day period showed only a slight decrease in the number of plants coming up in the seed-flats, as compared to the germinator methods. This fact, combined with the relative ease of running large numbers of tests in trays, as compared to seed-flats, led to the selection of the first method.

LONG-TIME STORAGE AT LOW TEMPERATURE

For the series of tests requiring long-time storage, two samples of bulblets of *Allium vineale* collected in 1951 were used. A single sample of *Allium canadense* was available. The bulblets were placed in small manila envelopes and kept in mason jars with loosely-placed glass covers, permitting air movement. The bulblets were exposed to room temperature, 72 ± 2°F. to 33°F. in an ordinary household refrigerator, and to 40°F. in a cold storage room.

Germination tests were run at about one-month intervals.

When stored at low temperatures (Table I), *Allium vineale,* harvested June 12, 1951, failed to show any germination during the trials. The bulblets held at room temperature broke dormancy in mid-November 1951, after about five months' storage. On the other hand, *Allium canadense,* harvested July 15, 1951, when held in cold storage and in the refrigerator, broke dormancy after two and one-half months. The bulblets held at room temperature broke dormancy in early January 1952, and remained consistently below the other two treatments in germination percent. The 40°F. temperature resulted in a higher germination percentage than the 33°F. temperature.

TABLE I.—The effect of prolonged storage at different temperatures on the germination of bulblets. Figures represent mean germination of two lots of 100 bulblets.

Lot[1] No.	Treatment	1951 Sep. 17	Oct. 18	Nov. 18	1952 Jan. 2	Jan. 30	Mar. 1	Mar. 28
	Allium vineale							
1	72°F.±2°	0	0	9.0	17.5	23.5	20.0	15.0
	33°F.	0	0	0	0	0	0	0
	40°F.	0	0	0	0	0	0	0
8	72°F.±2°	0	0	26.5	36.5	35.5	31.0	24.0
	33°F.	0	0	0	0	0	0	0
	40°F.	0	0	0	0	0	0	0
	Allium canadense							
	72°F.±2°	0	0	0	2	7.5	11.0	8.0
	33°F.	0	2.5	2.5	12.5	20.5	25.5	16.0
	40°F.	6	7.0	14.5	32.5	35.5	30.5	9.5

[1] All specimens were collected in the summer of 1951.

AGING AND VIABILITY

The span of viability of bulblets of these species is of interest to seedsmen who store grain and grass seed for some length of time. In order to determine how long a period would elapse before the bulblets would no longer be capable of germination, twenty-nine lots of *Allium vineale* collected from 1943 to 1950, and stored at room temperature, were tested in 1951. Fourteen lots, collected in the years 1943 through 1949, failed to germinate when tested in February; two other lots (one collected in 1948, the other 1949) had low germination percentages (see below). Similar samples of 5 lots of *Allium canadense* collected in 1945, 1948, and 1949 were tested, but none germinated.

All of the bulblets of *Allium vineale,* collected in 1950, (except Lot 79) germinated when first tested in February 1951; in April, four of the twelve 1950 samples were dead; in July, seven samples no longer were viable, and by March, 1952 only one lot was still capable of germination (Table II). This lot no longer germinated when tested in April.

One (Lot 40) of the three samples collected in 1949 germinated when first tested in February, 1951. In March it was dead. One (Lot 36) of the six samples collected in 1948 displayed weak germination (2%) when tested in February, 1951, and none after that. The bulblets collected before 1948 were dead in February, 1951; these included 3 lots in 1943, 2 lots in 1944 and 2 lots in 1945.

It is of interest to note (Table I) that maximum germination was

TABLE II.—The loss of viability of bulblets of *Allium vineale* with the lapse of time.

Lot No.	Harvest Date	1951 Feb.	1951 Apr.	1951 Jul.	1951 Sep.	1952 Mar.	1952 Apr.
		Germination percentage					
11	1950	13	1	0	0	0	0
12	1950	22	0	0	0	0	0
13	1950	38	4	3	1	0	0
15	1950	12	0	0	0	0	0
16	1950	7	0	0	0	0	0
17	1950	17	0	0	0	0	0
72	1950	42	6	0	0	0	0
73	1950	43	21	3	0	0	0
74	1950	44	9	0	0	0	0
75	1950	49	26	5	2	0	0
77	1950	42	14	4	2	0	0
78	1950	72	33	4	6	2	0
79	1950	*	*	*	*	0	0
40	1949	18	0	0	0	0	0
36	1948	2	0	0	0	0	0

* Not tested at this time.

reached within five to six months after harvest, followed by a steady decline. This is true of *A. vineale* (Table I), and is evident with *A. canadense* in cold storage.

BULBLET SHRINKAGE

Effect on Germination.—A morphological characteristic often suggested by seedsmen to distinguish between bulblets capable of germination and those not capable of growth, is size; a number of farmers and seedsmen suggest that small bulblets will not germinate.

In order to test this hypothesis, selections of bulblets were made, according to size, i.e., small, large or medium. They were then weighed and length and width were measured. The width was the measurement of the widest point on the bulblet. There was a direct relationship between size and germination (Table III). These tests were made in February 1951.

During the summer of 1951 other tests were set up with fresh material of the two species. For *Allium vineale* three lots were selected and each was arbitrarily divided into four samples, two of large and two of small bulblets; the same technique was used for *Allium canadense*. The material was stored in small manila envelopes at room temperature.

In every case except one (Lot 9) the large bulblets reached a greater maximum germination than did the small; in all cases in both species the larger bulblets maintained their viability at a higher percentage for a longer period of time (Table IV).

Although Lot 95 (Table IV) contained the smallest bulblets of any tested, it reached a higher germination percentage than any of the lots tested. The only nonviable sample at the end of the experiment was Lot 14S which contained the largest of the small bulblets used.

The bulblets of *Allium canadense* behaved in a similar manner, with the large bulblets breaking dormancy first, and reaching a higher maximum than the small bulblets.

During the germination tests, the various samples of bulblets were weighed to assay the loss of moisture, in order to determine whether there was any correlation between such loss and germination per-

TABLE III.—The relationship between size of bulblets and germination of *Allium vineale*. Each figure represents the mean for 100 bulblets.

Description	Mean weight in mgms	Mean size in cms	Mean percent germination
Small	1.63	0.39 x 0.21	10.0
Medium	3.56	0.54 x 0.23	28.0
Large	7.99	0.64 x 0.27	44.2
Random	----	----	26.5

TABLE IV.—The relationship between bulblet size and percent germination of *Allium vineale* and *Allium canadense*. Each figure represents the mean of two lots of 100 bulblets each. Harvested summer, 1951. (S = small, L = large).

Lot No.	Mean wgt. mgms. per bulblet	1951 Nov. 18	1952 Jan. 2	Jan. 30	Mar. 1	Apr. 2
		Allium vineale				
14S	10.2	0	14	0	0	0
14L	26.5	12	34	24	15	3
9S	2.1	15	78	33	35	5
9L	10.6	30	63	65	59	23
2S	7.3	12	26	30	34	12
2L	25.8	41	32	62	51	22
		Allium canadense				
S	19.7	0	9	4	2	4
L	43.2	16	25	38	55	52

centage. There was a greater average loss of moisture from the small bulblets of *Allium vineale* than from the large ones, but no appreciable difference in *Allium canadense.*

Within the *Allium vineale* series, Lot 9S reached the highest germination percentage (Table IV), and had the greatest water loss (Table V). Lot 9L exhibited the second highest rate of germination,

TABLE V.—A comparison of the moisture loss between small and large bulblets of *Allium vineale* and *Allium canadense* over a nine-month period of time. Each figure represents the mean weight (in mgms) of five hundred bulblets. Collected summer of 1951.

Lot. No. or Sample	1951 Jun. 22	Jul. 19	Sep. 7	Nov. 17	1952 Jan. 20	Mar. 27	% loss of orig. wgt.
			Allium vineale				
2S	0.732	0.680	0.645	0.584	0.521	0.452	38.29
2L	2.581	2.240	2.233	2.149	1.984	1.634	36.70
9S	0.413	0.320	0.305	0.302	0.219	0.159	61.41
9L	3.188	2.884	2.854	2.136	2.013	1.948	38.89
14S	0.203	0.134	0.122	0.111	0.092	0.085	57.97
14L	0.530	0.378	0.353	0.297	0.231	0.199	62.45
			Allium canadense				
small			2.298[2]			0.036	59.2
small			3.185			1.349	57.6
large			13.554			6.036	55.2
large			12.811			5.892	54.0

[2] Measurements taken July 28.

but had a very low rate of moisture loss. Obviously there is no relation between water loss and germination.

Bulblet Shrinkage and Re-cleaning Seed.—The idea that the outer paper covering of bulblets of *Allium vineale* remains distended while shrinkage takes place in the inner fleshy portion had been suggested in an early work (Duvel, 1907), but no data were presented to support the claim.

A group of bulblets, screened to remove the very smallest (less than 0.18 cm in diameter) and the very largest, was selected to provide the material for a test. Fifteen medium-sized bulblets with the covering intact, and fifteen with the covering removed, were used. Each individual bulblet was placed in a paper envelope, and measurements of the long axis, and the widest part of the short axis, were made at monthly intervals. The first measurement was July 16, 1951, one day after harvest. Repeated measurements were made in August, September, and October. On the last two dates there were no discernible changes.

The decrease in measurable size was negligible when bulblets with the coverings were measured, but there was a significant decrease with the naked bulblets (Table VI).

This emphasizes the fact that re-screening some time after seed harvest is a practical method of reducing the number of bulblets present in crop seeds.

CROP SEED STORED WITH BULBLETS

Crop seed, such as wheat (*Triticum aestivum* L.), crimson clover (*Trifolium incarnatum* L.), and orchard grass (*Dactylis glomerata* L.) are often stored over winter with bulblets of wild onion and wild garlic, because of the impossibility of securing complete removal. The occurrence of some injury to the crop seed from the volatile oils present in the *Allium* is a possibility. The following experiment was designed to determine whether such an effect was present.

Fifty bulblets of each species were mixed with one pound lots of clover and wheat, and stored in separate glass containers, stopped with cotton plugs, from August 1951 to March 1952. In only one instance was there any obvious effect on germination of a crop seed. The

TABLE VI.—A comparison between shrinkage of bulblets of *Allium vineale* with papery outer covering and without papery outer covering (measured in cms).

	With covering		Without covering	
	Length	Width	Length	Width
July 16	.653	.297	.549	.287
August 16	.645	.293	.495	.257
Shrinkage	0.2%	2.0%	9.8%	10.4%

presence of *Allium vineale* apparently slowed the rate of germination of wheat seed during the first 48 hours, but at the end of 96 hours there was no difference in germination of the test material as compared to the control. Two replicate lots of 100 seeds each were used.

The storage of crop seeds with bulblets of wild onion and wild garlic appears to have no harmful effects on crop seed germination.

EFFECT OF MECHANICAL INJURY ON GERMINATION

Injury by Rolling.—A number of seed houses pass seeds through rollers, particularly those with hard seed coats, such as the clovers, in an effort to crush and kill the bulblets mixed with them. A large sample of crimson clover seed (*Trifolium incarnatum*) so treated was made available by a seed house for testing. The bulblets present were very small and were tested in March and July 1951, using ten replicates of 100 bulblets each time. In no case was there any bulblet germination. The seeds had been rolled during the winter of 1950-51.

In the early spring of 1951 four samples of *Allium vineale* collected the previous summer were treated in the same scarifier, two going through once, and replicates going through twice. Those rolled once showed no marked change in germination (avg. 59%) from controls (avg. 64%), whereas those rolled twice showed a marked decrease (avg. 31%) in germination (Table VII). Apparently rolling bulblets once has little effect on germination, while rolling bulblets twice causes severe damage and results in decreased germination.

Cutting Bulblets.—Bulblets of wild garlic and wild onion showing injury to the basal end were considered as inert matter, incapable of germination.

The results of original work (Bass and Hooker, 1941; Hooker, 1942) are somewhat confusing, as in the first case, cutting bulblets resulted in failure to germinate, while the later tests by Hooker in 1942, showed that basal portions of bulblets of *Allium vineale,* as well as longitudinal portions were capable of developing.

In order to determine whether or not bulblets with either basal or apical portions missing were capable of germination, four lots of 100 bulblets of *Allium vineale* were utilized immediately after harvest in July 1951. Each bulblet in half of the sample was cut transversely. The bulblets in the other half of the sample were cut longitudinally. This treatment was repeated with a sample of *Allium canadense*. All

TABLE VII.—The effect of rolling injury on germination of bulblets. Each figure represents the mean percent germination of four lots of 100 bulblets each.

Species	Rolled once	Rolled twice	Control
A. vineale	45.0	20.0	66.0
	73.0	42.5	61.0
A. canadense	60.5	31.0	56.0

bulblet pieces of both species failed to germinate when tested in December 1951 and March 1952.

On March 28, 1952 the treatments were repeated, using bulblets from the original treated lots of both species, but the amounts of basal and apical portions left were varied. It will be noted (Table VIII) that when the lower or basal portion is missing on the bulblets of either species there is no germination (Fig. 2), but that when parts of the apical end are removed, the basal portions are fully capable of germination (Fig. 3).

There was a direct correlation between germination and the amount of basal portion left, suggesting the presence of a "meristematic" region at the base.

The very significant increase in germination obtained by cutting the bulblets in half, longitudinally, (Table VIII) can better be appreciated when it is noted that the figures representing percentage germination for the treatment are an average figure for *both* halves. Thus under Lot 7, the figure 83 percent means that a total of 166 plants were produced from 200 pieces.

The failure in germination of bulblets cut in June 1951, and tested some months later, might well be due to excess drying, the result of moisture loss from the surfaces; there also might be a question of physiological maturity. When the bulblets are collected, it is possible that there is a period of after-ripening during which foods, or perhaps auxins, move from the apical end to the basal portion of the bulblets, and that cutting before this transfer occurs, inhibits germination.

GERMINATION OF RED AND WHITE BULBLETS

The question has been frequently raised by seedmen as to the viability of white or greenish bulblets of *Allium vineale,* which they consider as being immature, and that of those bulblets exhibiting red coloring which are considered mature. One early worker (Watts, 1895) claimed to have secured 95 percent germination of immature bulblets,

TABLE VIII.—Germination of portions of bulblets cut immediately before tests, March 28, 1952 (100 bulblets cut in each test; results expressed as percent of total pieces germinating).

Portion tested	*Allium vineale* No. 2	No. 5	No. 7	No. 9	*Allium canadense*	
Upper 1/3	—	—	0	0	—	0
Upper 1/2	0	0	0	0	0	0
Upper 2/3	—	—	0	0	—	0
Lower 1/3	—	—	34	21	—	10
Lower 1/2	100	100	75	64	13	15
Lower 2/3	—	—	94	63	—	14
Longitudinal Halves	100	95	83	79	37	32
Control uncut	30	0	88	54	26	28

although he did not define his criterion of maturity. For the tests indicated below, bulblets with the papery covering intact were used as "colorless" specimens (see Fig. 1).

The red coloring matter found on some bulblets is generally at the apical, rounded portion, whereas the basal end, attached to the stem is usually lacking in this color. In unpublished work, where running tap water was used to break dormancy, it was found that the red coloring matter is water soluble.

The data presented in Table IX show that red bulblets broke dormancy earlier and reached a significantly higher germination than did the colorless bulblets.

At the beginning of this experiment bulblets were selected for approximately equal weight (Table X). During the course of the experiment the bulblets were weighed at intervals to determine the loss of moisture. The red bulblets lost a larger percentage than did the white or green bulblets (Table X).

It is concluded that colorless bulblets are capable of germinating and must be considered as noxious weed "seeds."

BULBLET COMPOSITION

Material collected during the summer of 1951 was analyzed immediately after harvest to determine the percentages of moisture, or-

TABLE IX.—Germination percentage of red bulblets compared to white bulblets harvested in the same field on the same day (June 12, 1951). Figures are mean germination of 2 lots of 100 bulblets each.

	1951			1952	
Sample	Oct. 18	Dec. 20	Jan. 30	Mar. 1	Mar. 28
Red	1.0	16.0	24.5	26.0	26.0
White	0	0	0	1.5	1.5

Fig. 2.—Failure of development of the apical portion of bulblets (upper row, *A. canadense;* lower row, *A. vineale*). Photograph taken two weeks after cutting.

ganic matter and ash. The moisture content was determined by weighing duplicate lots of 100 bulblets after placing them in forced draft ovens for four days at 85°F. The difference between the dry weight and original fresh weight was calculated on a percentage basis. The bulblets were then ashed in a muffle furnace at 450°F. for twenty-four hours, and the final weight taken as the amount of ash. The difference between the final weight and oven dry weight was taken to be organic matter.

For *Allium vineale* the amount of water present was found to be fairly uniform, varying from a low of 55.9 percent to a high of 62.5 percent. Previous tests (Cox, 1916) have shown a far lower moisture content, with a minimum of 25.9 percent, a maximum of 41.7 percent, and an average of 37.9 percent. There was no indication given in his paper as to the elapse of time between harvest and the determinations.

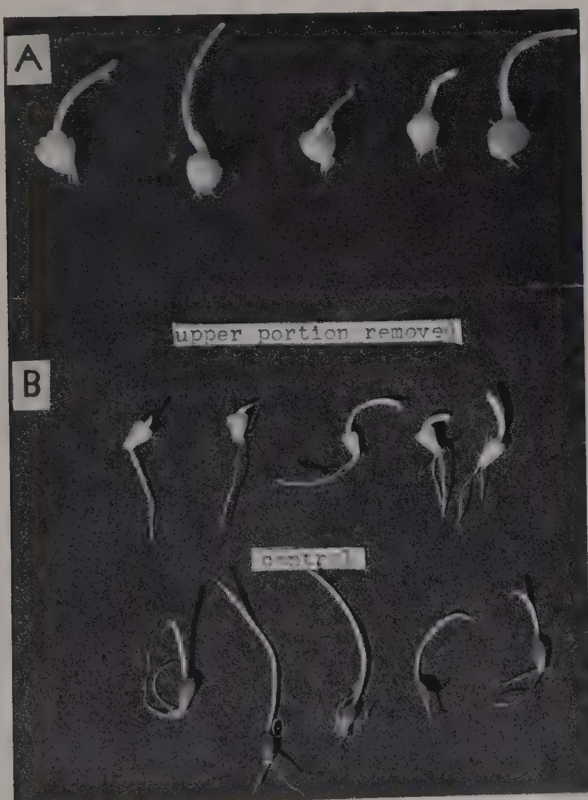

Fig. 3.—The normal development of bulblets with the apical end removed. A. — *A. canadense*. B. — Experimental and control, *A. vineale*. Photographs taken 2 weeks after cutting.

TABLE X.—A comparison of the weight loss (moisture) in mgm per bulblet between red bulblets and white bulblets of *Allium vineale* harvested in the same field on the same date, June 12, 1951. Each figure is the mean weight of 200 bulblets.

Sample	Jun. 22	Jul. 19	Sep. 7	Nov. 17	Jan. 20	Mar. 27	% of original weight
Red	1.687	1.543	1.467	1.343	1.218	1.040	61.6
White	1.857	1.848	1.691	1.646	1.527	1.364	73.4

Organic matter for *Allium vineale* varied from a low of 37.2 to a high of 43.0 percent; ash from a low of 0.3 percent to a high of 3.6. Analysis of results indicated that size of bulblets was in no way correlated with moisture content, ash or organic matter.

Bulblets of *Allium canadense* were separated into groups, according to size, and analyzed. Small and large bulblets had the same general composition.

CONCLUSIONS

Freshly harvested bulblets of *Allium vineale* placed at storage temperatures of 33°F. and 40°F. were dead after five months; bulblets of *Allium canadense* had the dormancy period shortened by storage of 33°F. and 40°F.; bulblets of both species are incapable of germination after storage at room temperature for three years.

Small bulblets of both species have a lower germination rate than do large bulblets; small bulblets of *Allium vineale* lose viability more rapidly than do large bulblets.

Shrinkage of the fleshy portion of the bulblet is considerably greater than shrinkage of the papery outer covering; serious injury decreases germination of both species; basal and longitudinal sections of bulblets of both species are capable of germination, upper portions are not; bulblets of *Allium vineale* lacking red color are capable of germination, but at a lower rate than red bulblets.

Wheat (*Triticum aestivum* L.) and crimson clover seeds (*Trifolium incarnatum* L.) are not harmed by storage with bulblets of either species.

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Book Reviews

THE VIRUSES. Biochemical, Biological and Biophysical Properties. Volume 3. Animal Viruses. Edited by F. M. Burnet and W. M. Stanley. Academic Press, New York City. 1959. $12.00.

This is the third in a three-volume work and is the first to appear. As a general observation, the work is well-organized. Each chapter is written by an established investigator and most of the chapters are well-written. All are inclusive.

The new classification proposed is in line with recent information in virology and follows the recommendation of the various international committee meetings for nomenclature and classification held during the past few years. One small item of error which shows the rapidity of movement in the field of virology involves the inclusion of the psittocosis group as a virus. This group is now considered in the rickettsia.

The chapters on hemagglutination by S. G. Anderson and on the morphological approach by F. B. Berg present the field in a broken fashion under the classification of each group. This reviewer considers such a method stereotyped. One finds himself reading the stilted compilation, sentence by sentence, point by point, investigator by investigator, until the only way one can be sure of the point the author is trying to make is to refer back to the paragraph title, which is conveniently printed in italics.

The other chapters, 13 in all, are not quite so stilted and Chapter VI on intracellular growth by Alick Isaacs is worth the price of the book.

The bibliographic method is a poor one. It forces the reader to skip over parentheses in almost every sentence. Since this is a book, it seems to this reviewer that a small number in parentheses in lieu of the author's name and the publication date could suffice. The number would obviously refer to the bibliography for the chapter.

Further, it would be so much better if scientific writers would learn to write prose instead of an "outlinish" type of sentence and paragraph structure.

All in all the volume is a worthy effort. It is recommended as a source document but not for reading.—THOMAS G. WARD, University of Notre Dame, Notre Dame, Indiana.

UTILIZATION OF NITROGEN AND ITS COMPOUNDS BY PLANTS. Symposia of the Society for Experimental Biology, Number 13, edited by H. K. Porter. Academic Press, Inc., New York, 1959. 385 pp., $9.50.

This volume, containing a total of 20 papers presented at the University of Reading in September of 1958, upholds the high standards of preceding symposia published by the Society and provides a broad review of various aspects of nitrogen utilization by plants. It is of interest that the included papers are by authors from Australia, England, Finland, Germany, New Zealand, Russia and the United States. The symposium as a whole underlines the need for clarifying biochemical mechanisms involved in nitrogen utilization and, further, makes apparent that an understanding of the physiological integration of such mechanisms in the living organism as a whole is only now being approached.

Possible biochemical steps and mechanisms involved in the reduction of nitrate, nitrite and other proposed intermediates in the over-all process of nitrate reduction are discussed by Nicholas in the first paper. Much of the available biochemical information in this area has been obtained from bacteria and fungi which, along with studies on algae discussed in the present symposium by

Kessler, accent the contribution which microorganisms can make to our understanding of higher plants and animals. Roberts provides an excellent discussion of the chemistry of the still-challenging process of nitrogen fixation, exploring the reasons for considering more thoroughly an oxidative first step; and Bond describes an interesting and not widely recognized group of non-legume plants which form root nodules and fix nitrogen. Amino acid formation and participation in protein synthesis in both yeast and barley, based largely on previously unpublished kinetic data collected at the University of Bristol, is described by Folkes. His remarks about alternatives to the hypothesis which considers that amino acids are formed following nitrogen uptake and then function as direct precursors of protein serve only to emphasize that today little practical validity can be attached to such alternatives. Steward describes the variety of changes which may occur in the amino acids and amides of the cell sap, and thus the physiological complexity of such changes, as environmental and nutritional conditions are varied. Present knowledge of the mechanics of amide and peptide bond synthesis — basic to mechanisms of protein synthesis — is reviewed by Webster, and the possible role of ribonucleic acid in the synthesis of protein is discussed by Heyes on the basis of studies with cultured pea roots. An unbalance in the symposium is marked by the inclusion of only a single paper concerned with the nucleic acids. Considering more specialized compounds, Mothes gives a thorough review of recent knowledge of alkaloid biosynthesis; and Fowden discusses the implications for plant physiology of a variety of newly discovered amino acids.

Though a great amount of information is summarized, wide gaps in our knowledge of nitrogen utilization become evident in the papers presented. A statement by Roberts in discussing nitrogen fixation might be considered an appropriate summary to the whole subject of the symposium. ". . . the number of proposed metabolic routes and mechanisms that are consistent with all the data is very limited; even so, none is proven, and the truth must await the gradual closing in of the attack from several different points." — EDWARD SPOERL, U. S. Army Medical Research Laboratory, Fort Knox, Kentucky.

FLORA OF ALBERTA. A manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the province of Alberta, Canada. By E. H. Moss. University of Toronto Press, Toronto, Ontario. viii + 534 pp. 1959. $10.00.

The publication of *Flora of Alberta* is a major event in North American floristic botany. Alberta, which is larger than Illinois, Indiana, Ohio, Michigan, and Wisconsin combined, is a region of great botanical interest and one that has long been in need of a comprehensive flora. It is the meeting ground of grassland and forest and of Cordilleran and boreal elements. In the extreme northeastern part of the province begins a transition from boreal to arctic. Among the floristic works usable in Alberta, the most noteworthy are Rydberg's much out-of-date "Flora of the Rocky Mountains and Adjacent Plains" (1922), including only the southern half of the province, and Budd's "Wild Plants of the Canadian Prairies" (1957), serving well in the prairie and parkland areas.

Dr. Moss's *Flora of Alberta,* the first to cover the entire province, fills admirably the need for such a work and will be indispensable for all students of the plants of Alberta and surrounding regions. The author, professor emeritus of botany at the University of Alberta, is amply qualified to write a flora of the province whose plants he has studied for some thirty-five years. In addition to the present volume, his *opus magnum,* Dr. Moss has written a series of excel-

lent articles on vegetation of the province and also a review, "The Vegetation of Alberta," which appeared in *Botanical Review* in 1955.

The main part of the Flora, following a brief and botanically uninformative preface, consist of well-constructed keys to and concise descriptions of 499 genera, 1,605 species, and 215 taxa of subspecific rank, included in 104 families of vascular plants. The more frequently encountered synonyms are listed, as are also common names when these "are known to have a considerable degree of currency." The arrangement of families is based on the Englerian system, but genera and species are arranged alphabetically to facilitate "locating genera within families and species within genera." Included are a few species not at present known in Alberta but which will "almost certainly" be found there. A glossary, a bibliography, and an index bring the book to a close.

A second edition of *Flora of Alberta* would benefit by the inclusion of more explicit distribution data — the present data are mostly so general that they are of little use to the reader who wants to know where in Alberta the various species occur. Also helpful would be the addition of brief sections on the geology, physiography, climate, vegetation, and history of floristic study of Alberta.

The book is sturdily and attractively bound and is well printed, on thin but strong paper, with an exceptionally readable type. The use of an especially prominent bold-face type for scientific names is most welcome. The *Flora of Alberta* is a highly valuable, taxonomically up-to-date, and much needed work. Dr. Moss and the University of Toronto Press deserve our heartiest thanks and congratulations for a job well done. — JOHN W. THIERET, Chicago Natural History Museum.

HANDBOOK OF GASTROPODS IN KANSAS. By A. Byron Leonard. Museum of Natural History, University of Kansas, Lawrence, Kansas. 1959. Paper bound, $1.00, cloth bound, $2.00.

This is unquestionably the best conceived state handbook on snails yet published. The presentation of complete data on local distribution, copious ecological notes, and available data on life histories make this of use to the professional malacologist. The keys, general sections, and illustrations are intended to aid the amateur collector or general naturalist. Its plan may well serve as a model for others.

Unfortunately, the execution was not equal to the design, the book showing numerous signs of carelessness or just plain sloppy work. The illustrations are from generally poor photographs which have been heavily and crudely retouched, sometimes beyond the point of recognition. The figures on plate 11, for example, are grotesque parodies of the species they are supposed to represent. The introductory line drawings (figs. 1-19) are copied from other sources (without acknowledgment) or are extremely poor originals.

More important are several major errors of omission. The transmission date of the manuscript is given as April 30, 1959. Yet the general discussion on the classes of mollusks (pp. 13-14) does not mention the zoological discovery of the decade, the segmented mollusk *Neopilina*. Described in 1957, this creature has been pictured in *Life* and *Natural History*, mentioned several times in *Science*, and even in some textbooks. Similarly, the section on the Lymnaeidae (pp. 47-56) ignores Hubendick's 1955 monograph, and the discussion of *Pomatiopsis* (p. 35)fails to cite any of the numerous studies produced at the University of Michigan from 1956 to date. In the land snails, Archer's 1947 paper on *Stenotrema* and Webb's admittedly difficult studies on slugs were not consulted.

These omissions of well-known papers are understandable if the citation on the title page acknowledging "the technical assistance of E. J. Roscoe, L. D. Fairbanks, C. D. Miles, and Tong-Yun Ho" is understood. The degree of "technical assistance" can probably be measured by comparing the text of the "Handbook's" *Succinea* section with Miles' 1958 paper (Univ. Kansas Sci. Bul., 38:1499-1543, 1 pl., 10 figs.). The Leonard "Handbook" is a word for word copy, omitting only a few tables of measurements and some discussion sections. Nowhere is this stated.

The rest of the landsnail section was written by E. J. Roscoe and the freshwater snail section by L. D. Fairbanks and Tong-Yun Ho. It is, of course, impossible to know how much editing of these articles was done by Leonard. The large number of major errors of omission, however, would seem to argue that few changes and additions were made from the original manuscript. These errors, then, can be seen as the faults of beginning students.

It is perhaps more charitable to consider this a slipshod editorial job, than to believe that a zoologist of Dr. Leonard's position would be so unaware of developments in his own field.

The "Handbook" can be used by amateurs, although the glossary is inadequate to enable an amateur to use the keys, and the illustrations are unusable. It does contain much new locality data and is very well-designed and printed. It is a shame that its polished appearance contains so much inaccurate and sloppy work.

Finally, why the pretentious title "Handbook of gastropods in Kansas"? Why not a more widely understood "Handbook of snails in Kansas"? — ALAN SOLEM, Chicago Natural History Museum, Chicago, Illinois.

DRAWINGS OF BRITISH PLANTS Part XIII. Umbelliferae (2) Araliaceae. Cornaceae. 30 Plates. By Stella Ross-Craig. G. Bell & Sons, Ltd., London. 1959. 9/6. ($1.33).

This part presents the remaining 27 species in 16 genera of Umbelliferae native to the British Isles together with *Hedera helix* and 2 species in 2 genera of Cornaceae. Of the umbellifers, at least 8 species are cultivated, adventive or naturalized in this country, including the carrot, fennel, cow- and common parsnips, and garden angelica. *Hedera helix* (English Ivy) is well-known here and has been praised and vilified by gardeners across the country and often for the same reasons concerned with its growth habits. One of the two representatives of the Cornaceae, *Thelycrania sanguinea* (*Cornus sanguinea*) is a shrub frequently cultivated.

Beautiful, perspective views and magnified sections of flowers and fruits in addition to leaves, bristles and hairs, underground parts, and general characteristics of patterns of growth are shown in these drawings. The detailed and so clearly represented views of the floral parts, particularly, will be very helpful in identification and in becoming acquainted with some aspects of the morphology of these families.—L. G. KAVALJIAN, Sacramento State College, Sacramento, California.

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SYMPOSIUM: Speciation and Raciation in Cavernicoles[1]

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Introduction

THOMAS C. BARR, JR.
Tennessee Polytechnic Institute, Cookeville

Vast areas of the United States are underlain by caverniferous limestone. Conservatively estimated, there are at least 10,000 accessible caves in these limestone areas, with a collective total length of penetrable passages of fully 1,000 miles. Many caves, especially in (1) the Appalachian Valley and Plateau, (2) the Interior Low Plateaus, (3) the lime sink region of northern Florida, (4) the Ozark Plateau, and (5) the Edwards Plateau of Texas, are richly populated by animal life which, until recently, has received scant

[1] Presented at the 1959 Annual Meeting of the American Association for the Advancement of Science, December 28 sponsored by the National Speleological Society and the Society of Systematic Zoology. Arranged by Thomas C. Barr, Jr.

attention from American zoologists. Although the first obligatory cavernicoles from the United States were described in 1842 (DeKay) and 1844 (Tellkampf), cave faunas generated little interest until the explorations of A. S. Packard (compiled and summarized in 1888). North American cave vertebrates were surveyed by Eigenmann in 1909, but most invertebrates have been neglected. As late as 1931 Bolívar and Jeannel could write:

> . . . les naturalistes américaines n'ont enterpris aucune étude sérieuse de la faune de l'immense domaine souterraine qui s'offre à leurs investigations. On chercherait en vain dans les collections des Musées un seul cavernicole dont la capture date du XX^{e} siècle!

As the contributions of this symposium amply demonstrate, this situation no longer exists.

Obligatory cavernicoles exhibit an unusually striking correlation between structural modification and their peculiar environment, providing a ready source of material well suited for investigations in community dynamics, comparative physiology and ethology, evolution, and zoogeography. Such investigations presuppose a body of taxonomic information which, for most of the United States, has heretofore been wholly inadequate. Extensive collecting during the past decade and critical work by a number of specialists have resulted in rapid advances — principally, though not wholly, taxonomic in nature — in American biospeleology. Reviews of these advances in eight different groups of cavernicoles are brought together in the present symposium.[1]

The classification of cavernicoles, perhaps unfamiliar to American readers, employed by most of the contributors is that of Schiödte (1849) and Schiner (1853), modified and popularized in Europe by Racovitza (1907). *Troglobites* are animals found only in caves, except by accident (e.g., being washed out of caves by flooding of underground streams), and are so modified that they are unable to live outside of caves and associated solutional cavities. Examples are discussed by each symposium author. *Troglophiles* are animals found frequently in caves, reproducing there and completing their life cycles underground, but having no rudimentations restricting them to a cave existence. *Trogloxenes* are animals often found in caves, but not completing their whole life cycle underground. The best known examples are bats and cave crickets. The term *accidental* is usually applied to stray visitors, occurring fortuitously and fleetingly within caves. It should not be confused with *threshold trogloxene*, an expression properly reserved for a member of the array of animals habitually frequenting the twilight zone of caves.

The immediate problems facing biospeleology in the United

[1] The following paper is not available for publication at this time: T. L. Poulson: "The sequential development of cave adaptation in the Amblyopsidae." In addition, the paper delivered by C. H. Krekeler has been published elsewhere (see References, page 8).

States are those of discovering, collecting, and describing the troglobitic species. The present status of troglobite taxonomy can be ascertained by examination of the checklist prepared by Brother G. Nicholas and appended to this symposium. Approximately two hundred fifty species have been described. The greatest numbers of species are found in the Coleoptera (97), Amphipoda (34), Diplopoda (34), and Isopoda (24). The greatest numbers of individuals include these groups, plus the Collembola and Araneae.

Problems in the systematics of cavernicole turbellarians, crayfishes, millipedes, collembolans, rhadiniform carabids, pselaphids, pseudoscorpions, and opilionids are discussed in the papers which follow. Despite this wide coverage, at least nine troglobite groups of major importance are not represented in the symposium contributions.

(1) *Snails.* Undoubted troglobites occur in the families Amnicolidae and Pleuroceridae. One species of *Carychium* (Carychiidae) is an abundant terrestrial troglobite in the Mammoth Cave region. A number of species (some undescribed) of *Helicodiscus* (Endodontidae) and *Retinella* (Zonitidae) from Tennessee and Kentucky are troglophiles or troglobites.

(2) *Isopods* (Asellidae) and (3) *amphipods* (Gammaridae) can be found in almost any cave stream in the major caverniferous areas. The species of the latter are somewhat better known at present because of the work of Hubricht and Mackin (1940) and Hubricht (1943). The cave asellids demand considerable further investigation. Three trichoniscid (terrestrial), one ligiid (aquatic), and one cirolanid (aquatic) isopods have been described.

(4) *Spiders.* Most troglobite species of araneids in the United States belong to the families Linyphiidae and Nesticidae. Troglophiles and trogloxenes of other families are locally very abundant. A comprehensive study of North American cave spiders is being undertaken by Dr. W. J. Gertsch (pers. comm.), Department of Insects and Spiders, American Museum of Natural History.

(5) Five species of *Plusiocampa* (Campodeidae, Diplura) have been described from caves in the United States (Condé 1949). They occur in all of the major limestone areas.

(6) *Trechine beetles* (Carabidae). This large and significant group of troglobites is perhaps better known than any of the others, principally because of the work of J. Manson Valentine (1931, 1932, 1937, 1945, 1948, 1952). Jeannel (1949) revised the species known at that time, and additional genera and species have been added by Valentine (1952), Krekeler (1958), and Barr (1959a, 1959b, 1960a, 1960b). The largest genus, *Pseudanophthalmus*, is known from the Interior Low Plateaus and Appalachian Valley and Plateau in the eastern United States, from Pennsylvania to Georgia, and west to Indiana, Tennessee, and Kentucky. More than half of the described taxa are known from a single cave.

(7) The cavernicole beetles of the subgenus *Adelops* (*Ptomaphagus*, Catopidae) were revised by Jeannel (1949) and one species was added by Barr (1958). Eight troglobite and one troglophile species (*P. cavernicola* Schwarz) have been described. The troglobite species are most abundant in

northern Alabama and southern Tennessee, with one species each in central Tennessee and central Kentucky.

(8) *Amblyopsid fishes.* Three eyeless species are recognized in a revision of this family by Woods and Inger (1957). They are restricted to the Interior Low Plateaus and part of the Ozark Plateau.

(9) *Plethodontid salamanders.* The genera *Typhlotriton* and *Typhlomolge* have been known for more than sixty years. *Haideotriton wallacei* Carr was described in 1939. Of considerable interest are the recent discoveries of *Gyrinophilus palleucus* (McCrady 1954) and *Eurycea troglodytes* (Baker 1957). Whether *Typhlotriton nereus* Bishop or the various subspecies of *Eurycea neotenes* Bishop and Wright are to be considered troglobites or troglophiles seems debatable. The status of *Gyrinophilus lutescens* (Rafinesque) certainly cannot be satisfactorily determined without further study.

Little attention has been devoted to the ostracods, copepods, and other small aquatic crustaceans of the subterranean waters of the United States (Klie 1931; Chappuis 1931 and 1933). Among major groups of terrestrial cavernicoles, the abundant and diversified Acarina, at least some representatives of which occur in nearly every cave, have been almost wholly neglected.

Geographic isolation as a major factor in cavernicole speciation was stressed by nearly all the symposium contributors. Few other biotopes exhibit in so salient a manner the influence of extrinsic barriers to genetic continuity. The most spectacular cases of intense troglobite speciation are found among the beetles and the millipedes. Of 98 described species and subspecies of troglobite carabids, 54 are known only from a single cave. Twenty-eight are known from as many as 5 caves. Only 7 are known from 10 or more caves. Park (this symposium) gives similar data for the pselaphids. Similar estimates for cave millipedes are not yet possible. However, Causey (this symposium; pers. comm.) believes that the intensity of cave endemism in the millipede genus *Pseudotremia* (Cleidogonidae) approaches that of *Pseudanophthalmus* (Carabidae). The systematic picture emerging from study of such groups strongly suggests a dominant role for genetic drift, but the possibility of varying selection pressures in different cave systems has not been investigated.

By no means are all troglobites narrowly restricted in geographic distribution. On the contrary, there extends a spectrum of range size from the "one-cave-one-taxon" extreme to whole cave systems, groups of adjacent systems, physiographic provinces, and virtually the entire unglaciated Paleozoic limestone portion of the eastern United States. Even the cave carabids include a few surprisingly vagile species. *Neaphaenops tellkampfi* abounds in the Mammoth Cave district of west-central Kentucky and extends (with minor racial variations) northward to the Ohio River (Jeannel 1949) and southward to the Tennessee border (Barr 1959a). *Darlingtonea kentuckensis* — another large, cursorial species with similar habits — occurs in large numbers from Rockcastle County, Kentucky, southwestward along the ragged margin of the Cumberland Plateau into

northern Tennessee.[2] *Pseudanophthalmus tiresias* is a small, usually secretive species whose range is coextensive with the Central Basin of Tennessee, though local populations are subject to considerable geographic (supposedly subspecific) variation (Barr 1959a). Among the pselaphid beetles, two cavernicole species of *Batriasymmodes* (*spelaeus* and *quisnamus*) have such wide distributions that Park (this symposium) characterized them as "bothersome" because of the difficulty of explaining their subterranean dispersal by the usual means. In *Batriasymmodes,* however, the remarkably complex male genitalia provide virtual assurance of gene exchange throughout the known ranges of the species.

The more common aquatic troglobites have consistently more extensive ranges than most terrestrial troglobites, possibly because subterranean watercourses are less likely to be destroyed by erosion and collapse or blocked by silting and dripstone deposition, and probably because dispersal occurs beneath the water table under certain circumstances. The kenkiid planarian *Sphalloplana alabamensis* is known from the Cumberland Plateau of northern Alabama, northward into the Central Basin, Cumberland Plateau, and Appalachian Valley of Tennessee, in caves of the Cumberland and Tennessee River drainages (L. H. Hyman, pers. comm.). The amphipod *Stygobromus exilis,* described by Hubricht (1943) from the Mammoth Cave district, extends southward through central Tennessee into northern Alabama (L. Hubricht, pers. comm.). The eyeless crayfish *Orconectes pellucidus* is known from the Mitchell plain in southern Indiana, the western Pennyroyal Plateau of Kentucky, and the Cumberland Plateau of Kentucky, Tennessee, and Alabama. Five subspecies are recognized (Hobbs and Barr, in preparation). *Typhlichthys subterraneus,* the cave blindfish, is known from scattered colonies across central Kentucky and Tennessee to Missouri, Oklahoma, and northern Alabama (Woods and Inger 1957).

The most unusual and puzzling troglobite distributions, however, are those of the linyphiid cave spiders *Willibaldia cavernicola* (Missouri, Arkansas, Alabama, Georgia), *Bathyphantes weyeri* (Virginia, Kentucky), *Anthrobia monmouthia* (Kentucky, Tennessee, West Virginia), and *Phanetta subterranea* (Pennsylvania west to Indiana and south to Virginia, Tennessee, and Alabama).[3] It seems doubtful that such extensive ranges can be explained by dispersal through caves and solution crevices, yet none of these species is known from an epigean collection.

It is significant that six of the ten symposium participants mention the occurrence of related species in the same drainage system. That such a correlation should exist is quite probable in a limestone

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[2] Collected January, 1959, in Copperas Saltpeter Cave, Clinton Co., Ky., and Sells Cave, Fentress Co., Tenn. (T.C.B.); data from unpublished records.

[3] Distributions based on material collected by the writer and determined by W. J. Gertsch.

terrain, where subterranean erosions proceeds concomitantly with surface erosion, and many cave streams are demonstrable tributaries of surface streams. Dispersal of a troglobite species is thus believed to be facilitated by a ramifying network of solutional openings beneath the slopes of valleys occupied by surface streams (cf. Barr 1959a and this symposium; Park, this symposium). Yet so many serious anomalies arise when this concept is hard-pressed (most commonly the occurrence of one or two related species across a divide near the headwaters of an adjacent drainage system) that its pattern value may be critically questioned.

Although surface and subterranean erosion can and do take place in a limestone terrain simultaneously, they may not proceed at the same rate (Piper 1932), and surface and subterranean divides may not necessarily coincide. Furthermore, a large part of underground erosion is believed to take place beneath the water table (Bretz 1942). Terrestrial troglobites are distributed via the abandoned channels of ancient underground systems, the boundaries of which can conceivably overlap those of surface drainage basins. By a combination of overlap and underground stream piracy, hypothetical mechanisms can be elaborated by which a continuous system of solutional openings can extend completely through a limestone ridge separating two surface drainage basins. Ridges of insoluble clastic rocks, on the other hand, are very effective barriers. For example, the upper Elk River valley and the headwaters of Battle Creek are separated by the thick sandstones of the Cumberland Plateaus, which is less than three miles wide near Monteagle, Tennessee. On the west side of the Plateau (Elk drainage) the crayfish *Orconectes pellucidus australis* (Rhoades) and the cave fish *Typhlichthys subterraneus* Girard are abundant. In the Battle Creek valley caves years of exploration have never revealed *Typhlichthys.* Troglobitic crayfishes, though abundant, are not *Orconectes* but *Cambarus hamulatus* Cope and Packard (Hobbs and Barr, this symposium). Trechine carabids (*Pseudanophthalmus intermedius* Val., *P. lodingi humeralis* Val.) occur west of the Plateau, but a prolonged search for them in Battle Creek valley has been unproductive. When a limestone barrier is involved, the situation may be quite different. In the southeastern corner of the Central Basin of Tennessee, the valleys of the Elk and Duck Rivers are separated by Elk Ridge, composed of Ordovician limestone and capped with loose shale and chert. *Pseudanophthalmus tiresias tullahoma* Barr and an undescribed species of the millipede genus *Scoterpes* (det. by Nell B. Causey) occur in Duck valley caves in Coffee County and also in Elk valley caves in Bedford and Moore Counties. A distance of 12 to 15 miles intervenes.

Not only geomorphology but stratigraphy and geologic structure determine subterranean avenues of dispersal, and the student of cavernicole distribution can ill afford to ignore the contributions of these fields. Unfortunately for zoologists the investigation of cave origin and groundwater flow in limestone terrains is yet in its infancy For further details the reader is referred to the germinal works

of Cvijič (1918), Martel (1921), Davis (1931), Piper (1932), and Bretz (1942), and to the reviews of Warwick (1953), Thornbury (1954), and Barr (1954, 1960c).

The contributions of biospeleology to the study of geographic isolation and its effect on speciation are considerable, yet the foregoing observations suggest that the vagility of different animals and the variable, usually incompletely known extent of different cave systems must be taken into account in individual cases. Furthermore, it must be understood that any provisional conclusions or generalizations are (in most instances) predicated upon patently inadequate data. It may be unequivocally stated that more collections are needed in each group of troglobites now known from the United States. We need more specimens of most of the described species in order to determine the ranges of morphological variation. We need to know with considerable precision the geographic distribution of each taxon, requiring collections from as many caves as possible. *A priori* notions of the degree of isolation in individual caves must be abandoned, and taxonomic interpretation must rest on morphological and, where incontrovertible, geological evidence. Finally, it seems quite probable that a substantial number of the extant species of cavernicoles have not yet been collected. This extrapolation is justified in two ways: (1) repeated visits to biologically rather well-known caves have resulted in the discovery of rare, previously unknown species; and (2) there are still many cave areas in the United States which have never been thoroughly investigated by an experienced biospeleologist.

As stated near the beginning of this discussion, American biospeleology has not fully emerged from the stage of discovery and description of cavernicole species. The application of cave studies to basic ecological problems must be delayed until at least the preliminary foundation has been laid by taxonomy. To further such groundwork this symposium has been arranged. The following collection of papers might more properly be designated a "progress report" than a symposium. If, however, it serves as a spur to further investigation and, for a time, as an introduction to the study of North American cavernicole speciation, then its goal will have been achieved.

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Cave Planarians in the United States

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The occurrence of white, eyeless planarians in cave waters of the United States was discovered by A. S. Packard in an exploratory trip through the Mammoth and other Kentucky caves in May, 1874; but was not mentioned by him in print until 1880 when he gave the animal the name *Dendrocoelum percoecum.* It was not given a proper taxonomic study until 1931 when P. de Beauchamp, a French worker on Turbellaria, described specimens collected by C. Bolivar and R. Jeannel in their tour of North American caves in 1928. De Beauchamp ascertained that the worm is not a *Dendrocoelum* and in fact does not even belong to the family Dendrocoelidae. There are, in fact, no species of *Dendrocoelum* in the western world. De Beauchamp created for the worm the genus *Sphalloplana.* He pointed out that although the worm looks like a dendrocoelid its pharyngeal musculature conforms to the family Planariidae. It cannot be placed in this family, however, because it is provided with an adhesive organ. For this reason, I in 1937 created the family Kenkiidae for some of the white, eyeless planarians of cave waters of the United States.

Since the work of de Beauchamp, there have been found a number of additional species of planarians in the cave waters of the United States. There are now known a total of 14 species, two in the genus *Phagocata* of the family Planariidae, 10 in the family Kenkiidae, and two in the family Dendrocoelidae. It is the members of the Kenkiidae that merit further attention. All are white and eyeless and provided with an adhesive organ in the center of the anterior end. This organ shows within the family progressive stages of differentiation. In the genus *Sphalloplana* the adhesive organ is a shallow cushion in which the epidermis has been replaced by eosinophilous gland cells. A strong muscular provision enables the cushion to be moved in and out. In the genus *Speophila* the adhesive organ is a long tubular gland lined with eosinophilous glands and supplied with retractor muscles. The most remarkable of the adhesive organs occurs in *Kenkia rhynchida,* collected in an Oregon cave in 1934 by Carl Hubbs. This animal has a long snout occupied centrally by a long gland which is distally cyanophilous, proximally eosinophilous.

Remarkably enough, the adhesive organ shows the same stages of progressive differentiation in the Dendrocoelidae as in the Kenkiidae. Both the simple cushion-like stage of the organ and the deep tubular invagination are seen in genera of the Dendrocoelidae, although no counterpart of the condition in *Kenkia* has as yet been found among the Dendrocoelidae. We seem to have here a fine example of parallelism.

The cave planarians also illustrate to a marked degree speciation

as a result of geographic isolation. The same species may occur in caves relatively closely located, but caves separated by, say, the width of an average state have different species. In general, each state has a distinctive species. It is my belief that the Kenkiidae have evolved from the planariid genus *Phagocata* and through isolation in geographically separate caves have undergone extensive speciation.

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The Origins and Affinities of the Troglobitic Crayfishes of North America (Decapoda, Astacidae). I. The Genus Cambarus

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One of the most interesting phases of the history of crayfish dispersal and modification is that associated with the origins of troglobites. There are a few generalizations which can be drawn concerning the distributions and the origins of the several stocks which have engendered populations that have been able to meet the demands of a subterranean existence. In order to gain the proper perspective of the distributional relationships of the cavernicolous crayfishes with their epigean relatives, a brief summary of the distributions of the four genera with hypogean representatives is presented.

The largest genus in the family Astacidae, *Procambarus,* comprises more than 100 species and subspecies of which six are true troglobites. The range of the genus extends from Cuba, Guatemala and Honduras northward to Illinois and southern New England. Most of the species are found in the southeastern parts of the United States and Mexico where they are confined largely to the Coastal Plain and Piedmont Provinces. Only in Mexico have representatives been able to cross the divide into the Pacific drainage. The six albinistic species and subspecies are known only from Florida (4), Veracruz, Mexico (1), and Pinar del Rio, Cuba (1); that from the latter has not been described.

The monotypic genus *Troglocambarus* is known only from caves in the Florida peninsula.

The genus *Orconectes,* the second largest in the family, is composed of approximately 60 species and subspecies, and among them five troglobitic taxa have been recognized. The range of this genus is largely confined to the Mississippi and Great Lakes drainage systems, but a few species have reached the extreme southeastern part of the United States, and two occur east of the Appalachian system in an area extending from Maine to Virginia. The hypogean representatives are found in the Interior Low Plateaus of southern Indiana, central Kentucky and Tennessee, and northern Alabama.

The genus *Cambarus,* comprising some 40 species and subspecies, is represented by six troglobitic species within the United States. Its range extends from the Gulf of Mexico (Texas to northern Florida) to Canada; however, most of the species occur in the eastern part of the United States, along the slopes of and in streams arising in the Appalachian Mountains. The present discussion concerns the cavernicoles of this genus.

It is of interest that the genus *Cambarus*, which has the largest number of cave species (six), is smaller than *Procambarus* or *Orconectes*. This fact immediately poses the question of what factors, intrinsic or extrinsic, have favored the cambarids in their becoming established in subterranean waters a greater number of times than have the procambarid or orconectid stocks. Insufficient data are at present available to answer this question, for no comparative study of cavernicolous adaptations in crayfishes has yet been made. Until such data are available, explanations that may be offered are scarcely more than conjectures. It does seem appropriate to point out, however, that it is usually one of the species of *Cambarus* which causes the farmer difficulty with his spring. Apparently much of the life of the crayfishes frequenting springs is spent in tunneling about their mouths and exploring the subsurface channels from which the water issues. Furthermore there is considerable evidence that crayfishes have, through their burrowing powers, succeeded in diverting the flow of water away from its original exit, causing a spring to "go dry." As a result of such explorations in the sources of springs, animals may reach some of the large subterranean channels and pools. In some karst areas surface waters frequently have periodic or continuous communication with subterranean passages, thus providing ready access of hypogean habitats to most of the surface-dwelling crayfishes. Thus, the cambarids do not have exclusive "first rights" to the availability of spelaean habitats.

It is worthy of mention that two of the three areas in which the subterranean cambarids are known to occur are at the edge of the present range of the genus. Only *Cambarus latimanus* (LeConte, 1856:402), *Cambarus floridanus* Hobbs (1941:110), and *Cambarus diogenes diogenes* Girard (1852:88) have ranges that extend southeast of that of the albinistic *C. cryptodytes*, and their ranges extend less than 75 miles beyond it to the southeast. Only the ranges of *C. d. diogenes* and *C. hedgpethi* Hobbs (1948:224) extend west of those of *C. setosus* and *C. hubrichti*. The remaining three species, *C. hamulatus*, *C. jonesi*, and *C. cahni*, occur well within the range of the genus and perhaps not too far from its probable center of origin. It is puzzling that the large number of caves in the Appalachian Valley, the area which is dominated by cambarids, is devoid of albinistic crayfishes of any kind. In Barterbrook Cave, Augusta County, Virginia, occurs a small population of *C. bartonii bartonii* (Fabricius, 1758:407) in which the animals are distinctly lighter in color — cream and pale blue for the most part — but other than in reduced pigment, they are like the epigean forms. Specimens collected from a spring issuing from beneath the hill which houses the cave are typical in every respect. While this reduction of pigment is probably an ecophenotypic expression, there are no experimental data available to indicate that albinism in troglobitic crayfishes is not also ecophenotypic. The fact that pigment has been observed in both *Procambarus lucifugus alachua* (Hobbs, 1940: 402) where it occurs

in open sinkholes, and in *Cambarus setosus* (see below) at least opens the question as to whether or not the albinistic crayfishes are actually albinos in the usual sense.

Cambarus tenebrosus Hay (1902: 232), a pigmented species known from the Mammoth Cave region and to the south in Tennessee, frequently invades subterranean streams, but other than having smaller eyes than most surface-dwelling crayfishes, it exhibits no readily recognizable special modifications associated with cave life.

Cambarus cahni represents one of the most interesting forms which has found a congenial habitat in the subterranean waters. This species, reported only from Belgreen Cave, Franklin County, Alabama, is said by Rhoades (1941: 140) to be white with eyes "greatly reduced, though not to the extent found in *hamulatus*," and "is interesting because it shows affinities to both cave and surface forms" (*ibid.*: 141). Preserved specimens that are almost identical with the types of this species are available from several caves and streams in southern Tennessee and northern Alabama except that they are not white. Many of them were pale green, gray or tan, but the albinistic form has been reported only by Rhoades. The eyes of the types of *cahni* apparently are not any less well-developed than are they in the similar specimens from other caves in the area. Both *C. tenebrosus* and *C. cahni* are probably troglophiles.

THE ORIGIN OF THE TROGLOBITIC CAMBARID FAUNA

The troglobitic cambarids seem to fall into three distinct groups: the Extraneus Groups represented by *Cambarus hamulatus* and *C. jonesi;* the Tenebrosus Group, by *C. cahni* and *C. hubrichti;* and the Asperimanus Group, by *C. setosus* and *C. cryptodytes*. The groups are designated by the trivial names of the epigean species which seem to be close relatives of the hypogean forms. Thus it is suggested from the outset that the troglobitic cambarid assemblage is a polyphyletic one.

The areas inhabited by these crayfishes comprise three geographically disjunct cave regions: the Ozark region in which is found *C. setosus* and *C. hubrichti;* the Tennessee Valley in northern Alabama and southern Tennessee occupied by *C. hamulatus, C. jonesi,* and *C. cahni;* and the Florida Panhandle region, in which *C. cryptodytes* is the only representative, known from a single locality.

The Extraneus Group. — In this assemblage are found the most generalized members of the genus (Reasons for considering it thus are beyond the scope of the present paper but the reader is referred to Ortmann, 1905). The group is restricted to the eastern portions of the Tennessee and Cumberland drainage systems and the northern part of the Alabama drainage system. That *C. hamulatus* and *C. jonesi* are found in the cave region bordering the Tennessee River is not at all surprising. Both on morphological and distributional bases, it seems that *C. extraneus, C. hamulatus,* and *C. jonesi* share a common ancestry that is not too remote. The epigean *C. extraneus*

frequents moderate to large streams where the water flows rapidly over a rock-strewn bed.

Among the distinctive features that they share are rostra with well-defined marginal spines, relatively broad areolae, chelae that are not conspicuously setose (except in *jonesi*), and remarkably similar annuli ventrales.

The Tenebrosus Group. — Only four species belonging to this group have been described: *C. tenebrosus, C. ornatus* Rhoades (1944: 144), *C. hubrichti,* and *C. cahni.* The range of the group extends from the "lower Kentucky River drainage and short tributaries to the Ohio above Louisville" (Rhoades, 1944: 145) south and southeastward to northern Alabama. West of the Mississippi it is represented by *C. hubrichti.* The epigean forms, *C. tenebrosus* and *C. ornatus,* are encountered most frequently in springs, small headwater streams, and the former, in a number of caves within its range. There seems to be little doubt that *C. cahni* has been derived from a surface stock that was scarcely different from the southern form of *C. tenebrosus,* for as pointed out above, preserved specimens of the two species (in which the color has faded from the latter) are almost indistinguishable. Larger series of both from northern Alabama and southern Tennessee are needed to determine the limits of variation in both.

The affinities of *Cambarus hubrichti* are not quite so clear, for it apparently represents a relict form; at least its range is not contiguous with the known ranges of *C. tenebrosus* and *C. ornatus.* It is suggested that sometime during the Tertiary the range of the ancestral stock of the Tenebrosus Group extended westward from Kentucky and Tennessee to the eastern edge of the Ozark Plateau. What events occurred in the Pleistocene or Recent to bring about an annihilation of the epigean stock from the Mississippi Valley and the area to the west are not known, but it seems clear that a segment of it, *C. hubrichti,* was preserved in the subterranean waters.

These four species share the following characteristics: a broad areola which constitutes (usually) more than 38 percent of the entire length of the carapace; small eyes (very much reduced and without pigment in *C. hubrichti*); an elongate, rather robust chela that is not distinctly costate laterally, and without conspicuous groups of long setae.

The Asperimanus Group.—Typically, the members of this group frequent cool riffles or mountain streams. Although the range is a discontinuous one, most of the species occur in streams of the Western and Eastern Highland Rims of Tennessee, the Cumberland Plateau, and the Great Smoky Mountains. The albinistic *C. setosus* occurs in caves in southwestern Missouri and *C. cryptodytes* is found in one of the subterranean water systems of the Panhandle of Florida. These two troglobites are here considered to be relicts of a previously much more widely distributed stock. The Florida species, located several hundred miles south of the most southern limit of the range of pres-

ently existing epigean species of the group, suggests that its ancestors moved southward into southern Alabama or northern Florida during one or more glacial epochs of the Pleistocene. Assuming, tentatively, that such dispersal occurred, the epigean members may have been unable to survive the warming trend following glacial retreat. But a segment of this stock, the progenitors of *C. cryptodytes,* found a combination of tolerable environmental conditions in the subterranean waters of the northern portion of the Florida Panhandle. Perhaps it was also during the Pleistocene that the ancestors of *C. setosus* became established in the Ozark Plateau. It does not seem unreasonable to suppose that the ancestral stock attained the interior of the Ozark Plateau at the southern highly dissected margin of the Springfield upland by dispersal up the White River and into the James. Furthermore, if this route was followed, it seems probable that the stock moving into the area from the east would have had to cross what is now the Mississippi Valley before the river and the lower reaches of its tributaries became mud-bottomed streams, a type of habitat in which no member of the group is found at the present time.

Why *C. hubrichti* should occur only in the eastern part of the plateau and *C. setosus* in the west cannot be explained on the basis of available data. Various hypotheses may be advanced; for example, *setosus* may have colonized the caves earlier than *hubrichti,* the ancestors of which were unable to compete successfully with an established cavernicole species in the western part of the White River drainage, but were able to occupy a similar vacant niche in the eastern part of the plateau. There is little evidence to favor this over several alternative hypotheses.

The characteristics common to most of the members of the Asperimanus Group are: chelae with a single cristiform row of tubercles along the inner surface of the palm and with conspicuously setiferous fingers; setae long and often prominent on the palm; and the mesial process of the first pleopod usually elongate and frequently situated some distance proximal to the central projection.

KEY TO THE TROGLOBITIC CRAYFISHES OF THE GENUS CAMBARUS

1 Eyes with pigment .... *Cambarus cahni* Rhoades

1′ Eyes without pigment 2

2(1′) Rostrum without marginal spines and margins gently contracted cephalically so that acumen is not distinctly delimited basally .... *Cambarus cryptodytes* Hobbs

2′ Rostrum with or without marginal spines but margins always suddenly contracted so that acumen is distinctly delimited basally 3

3(2′) Areola more than 10 times longer than broad.... *Cambarus setosus* Faxon

3′ Areola less than 10 times longer than broad 4

4(3′) Chela with many long conspicuous setae.... *Cambarus jonesi,* sp. nov.

4′ Chela with few conspicuous setae, none of which are long 5

5(4′) Rostrum and postorbital ridges with prominent spines........................ .... *Cambarus hamulatus* (Cope and Packard)

5′ Rostrum and postorbital ridges with very small or obsolete spines .... *Cambarus hubrichti* Hobbs

ANNOTATED LIST OF SPECIES

Cambarus hamulatus (Cope and Packard)
(Figs. 1-10)

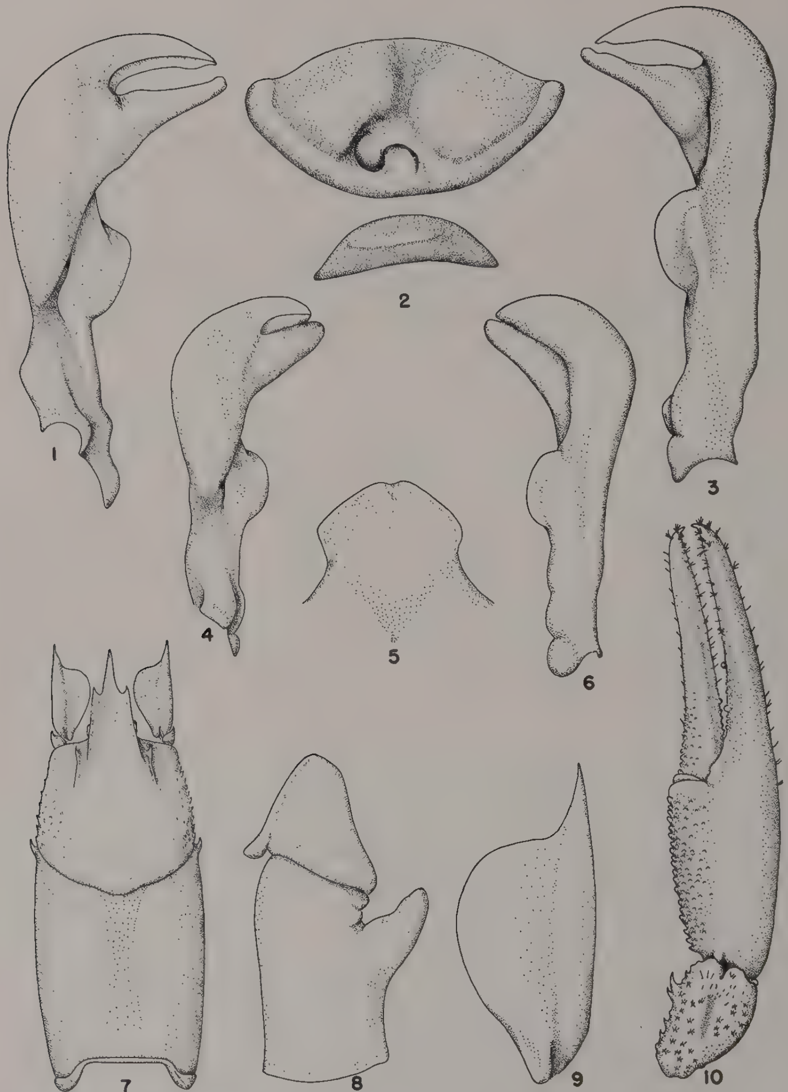
Orconectes hamulatus Cope and Packard 1881, Amer. Nat., 15:879, 880-882, Pl. VII, figs. 1, a-b.; Faxon 1884:145. [Type locality: Nickajack Cave, Marion County, Tennessee.]

Cambarus hamulatus Faxon 1884: 145; Faxon 1885: 7, 81-83, 43, 45, 59, 84, 85, 161, 170, 174, 3 figs.; Packard 1888: 40-42, 1 fig.; Faxon 1890: 628; Parker 1890: 154, 155; Lönnberg 1894a: 126; Lönnberg 1894b: 4, 5, 9; Hay 1899: 959, 966; Ortmann 1902: 277; Hay 1902: 435-437; Harris 1904: 59, 67, 101, 116, 151, 154, 162; Ortmann 1905: 118, 120, 121, 127; Faxon 1914: 422; Ortmann 1931: 95, 96; Creaser 1931: 6, 7; Fleming 1939: 299, 300, 301, 302, 303, 310, 311; Rhoades 1941: 146, 147, 148; Hobbs 1941: 114; Hobbs 1952: 689, 693.

Diagnosis.—Albinistic; eyes reduced and without pigment; rostrum with prominent marginal spines and a long acumen, margins only slightly converging, its upper surface concave without a median carina; postorbital ridges terminating cephalically in spines; areola broad and long, seven or eight times longer than broad and from 40 to 43 percent of the length of the carapace; one to several lateral spines present on each side of carapace; cephalolateral portion of carapace often with several small spiniform tubercles; chela not conspicuously setose but with ciliated tubercles, some of these arranged in several rows along inner surface of palm; hooks on ischiopodites of third pereiopods in male. First pleopod of male and annulus ventralis of female as figured.

Range.—*C. hamulatus* seems to be confined to the Sequatchie uplift near the juncture of the Tennessee and Sequatchie rivers. Tennessee—Marion County: Nickajack Cave (Cope and Packard, 1881); Winehouse Cave (Hay, 1902); Ship Cave, Coppinger Cove, Sequatchie River drainage (T.C.B.); Honeycutt Cave, Sweden's Cove, Tennessee River drainage by Battle Creek (T.C.B.); Speegle Saltpeter Cave, Speegle Cove, Tennessee River drainage by Battle Creek (T.C.B.); Lost Pig Cave, Sweden's Cove, Tennessee River drainage by Battle Creek (T.C.B.). Franklin County: Salt River Cave, Tennessee River drainage by Crow Creek (J.N. Dent; T.C.B.). [The record cited by Rhoades (1941: 148), Shelta Cavern, Huntsville, Madison County, Alabama is for *Cambarus jonesi* (see below)].

Remarks.—The stream in Nickajack Cave is very large, with a minimum channel depth (corrected for damming at mouth) of three feet, and is navigable for 2000 feet through a huge passage averaging 60 to 80 feet wide and 40 feet high. Before construction of Hales Bar and Guntersville Dams, the Tennessee River was subject to frequent flooding, and floodwaters backed up into the cave. There are no sand or gravel bars. In discussing the habits of *C. hamulatus* in Nickajack Cave, Hay (1902:435-436) states that "it was not until I began to look for them under rocks in the cave stream that I found how common they were. They appeared habitually to live under such, where they scooped out a cavity in which to lie and from which they



Figs. 1-10.—*Cambarus hamulatus*. 1. Mesial view of first pleopod of male, form I; 2. Annulus ventralis; 3. Lateral view of first pleopod of male, form I; 4. Mesial view of first pleopod of male, form II; 5. Epistome; 6. Lateral view of first pleopod of male, form II; 7. Dorsal view of carapace of male, form I; 8. Basipodite and ischiopodite of third pereiopod of male, form I; 9. Antennal scale; 10. Upper view of distal podomeres of cheliped of male, form I.

seemed seldom to travel. When disturbed, if they sought to escape, it was by crawling away rather than by swimming, and they would seldom move more than a few feet. Most often, however, they would lie perfectly still, and after the cloud of mud caused by raising the stone had cleared away, they could be seen lying quietly in their cavity or treading the mud to avoid being covered up. They were easily caught in the hands, as even after they had been touched they made no great effort to get out of danger. Indeed, in one case, I let a large specimen drop back into the water and a minute or so later found it lying at my feet; it had sunk like a stone and had not tried even to crawl away. They seemed to be totally devoid of the senses of sight and hearing, and the sense of touch did not seem to be nearly as well developed as in *C. pellucidus* [=*Orconectes p. pellucidus*]."

Cambarus jonesi,[1] sp. nov.
(Figs. 11-20)

?*Cambarus* (*Cambarus*) *hamulatus* Rhoades, 1941: 148 (in part).

Diagnosis.—Albinistic; eyes reduced and without pigment; rostrum with small marginal spines and acumen of moderate length, margins converging cephalically, its upper surface concave, without a median carina; postorbital ridges terminate cephalically in spines; areola broad and long, 5.4 to 6.8 times longer than broad with four to six punctations across narrowest part, and constituting from 41.2 to 44.9 percent of the length of the carapacc; a single lateral spine present on each side of carapace; cephalolateral portion of carapace granulate; chela studded with many conspicuous long setae; hooks on ischiopodites of third pereiopods in male. First pleopod of male terminating in two parts which are strongly recurved, with the apices of both terminals in the first form male directed proximocaudally. Annulus ventralis as figured.

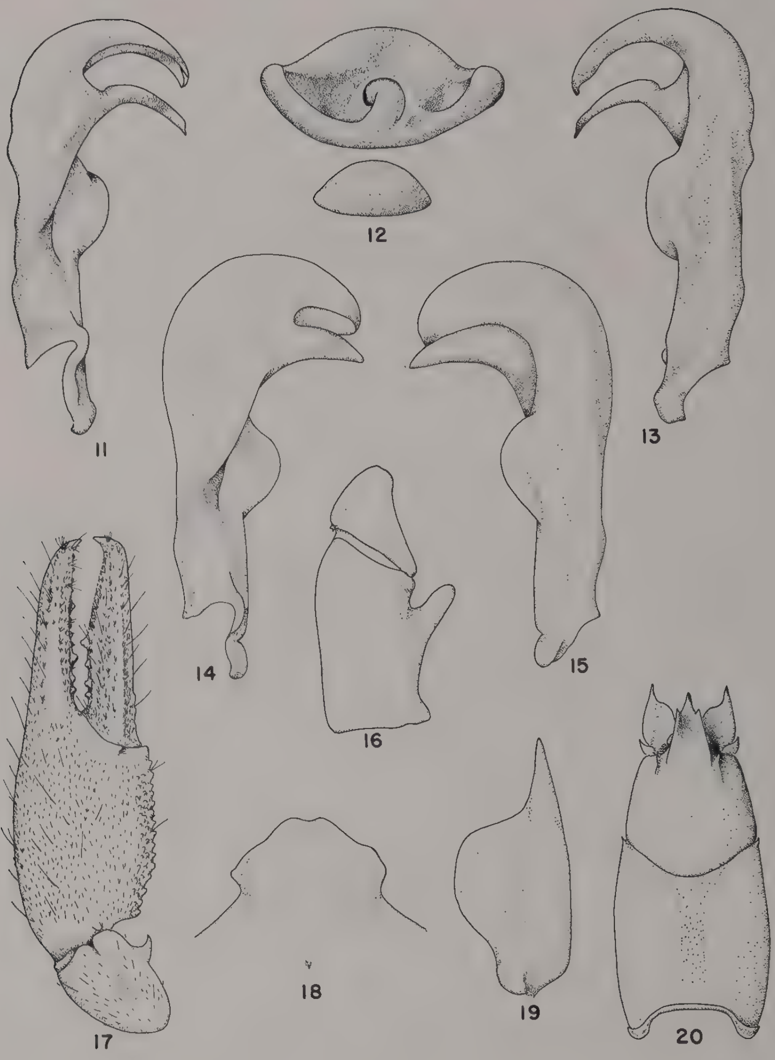
Holotypic Male, Form I.—Body subovate, slightly depressed. Abdomen narrower than thorax (8.9 and 10.7 mm in widest parts respectively). Width of carapace greater than depth in region of caudodorsal margin of cervical groove (10.2 and 7.8 mm). Greatest width of carapace near midlength of areola.

Areola moderately broad (5.5 times longer than wide) with five punctations across narrowest part; cephalic section of carapace about 1.4 times longer than areola; length of areola about 41.2 percent of entire length of carapace.

Rostrum with convergent margins which are only slightly thickened; small corneous marginal spines delimit base of corneous up-turned acumen which extends cephalad almost to distal margin of distal joint of peduncle of antennule; upper surface of rostrum concave with small setiferous punctations. Subrostral ridges weakly developed and evident in dorsal aspect for only a short distance at base of rostrum.

Postorbital ridges short and strongly depressed, grooved dorsolaterally, and

[1]It is with pleasure that we name this new species in honor of Dr. Walter B. Jones, Alabama State Geologist, who has contributed much to our knowledge of the geology and the fauna of the caves of Alabama.



Figs. 11-20.—*Cambarus jonesi,* sp. nov. 11. Mesial view of first pleopod of holotype; 12. Annulus ventralis of allotype; 13. Lateral view of first pleopod of holotype; 14. Mesial view of first pleopod of morphotype; 15. Lateral view of first pleopod of morphotype; 16. Basipodite and ischiopodite of third pereiopod of holotype; 17. Upper view of distal podomeres of cheliped of holotype; 18. Epistome of holotype; 19. Antennal scale of holotype; 20. Dorsal view of carapace of holotype.

produced cephalad in acute corneous spines. Suborbital angle lacking. Branchiostegal spine of moderate size and acute. Lateral surface of carapace with a small acute, corneous-tipped spine immediately caudal to cervical groove. Surface of carapace punctate except for weakly granulate cephalolateral portions.

Abdomen longer than carapace (25.0 and 22.6 mm). Cephalic section of telson with two spines in each caudolateral corner.

Epistome (Fig. 18) with a cephalomedian depression, with raised cephalolateral borders but without a cephalomedian projection. Antennules of the usual form with a prominent spine on ventral surface of basal segment. Antennae extend caudad slightly beyond caudal margin of telson. Antennal scale (Fig. 19) with a heavy lateral portion terminating in a long spine; lamellar portion comparatively short and broad.

Chela elongate (Fig. 17), subovate in cross section with palm slightly inflated; entire hand with scattered conspicuously-long setae. Inner surface of palm with tubercles forming four somewhat irregular rows, and a prominent tubercle on lower surface at base of dactyl; otherwise palmar area with setiferous punctations. Fingers not gaping. Upper surface of immovable finger with a submedian longitudinal ridge flanked laterally by deep setiferous punctations and mesially by somewhat shallower ones; lateral margin with a row of deep punctations each bearing one to several long setae; lower surface V-shaped in cross section and provided with two rows of long setae; opposable margin with a row of 11 knob-like tubercles of which the third and fifth from base are larger; usual large tubercle lying below this row present at base of distal third of finger; a single row of minute denticles extends along distal half of finger. Upper and lower surfaces of dactyl similar to corresponding surfaces of immovable finger, but mesial margin tuberculate proximally. Opposable margin of dactyl with a row of 15 rounded tubercles between which is a broken row of minute denticles; fourth tubercle from base largest.

Carpus longer than broad with a shallow longitudinal furrow above; entire surface of podomere with scattered setiferous punctations. Mesial surface with a large spine and lower mesiodistal margin with a similar one; two smaller tubercles present between the larger ones.

Merus with scattered setiferous punctations on all surfaces. Upper surface with a band of tubercles; band narrow proximally but broadens distally to extend on upper mesial and lateral surfaces of podomere. Lower surface of merus with a lateral row of 11 tubercles, ninth from base largest, and a mesial row of 13, the distalmost the largest. Ischium with a row of five tubercles along lower margin and a group of tubercles on upper margin.

Hooks on ischiopodites (Fig. 16) of third pereiopods only; hooks strong and simple. Coxa of fourth pereiopod with a prominent caudomesial protuberance.

First pleopod (Figs. 11, 13) extends cephalad to coxopodite of third pereiopod when abdomen is flexed. Tips terminating in two parts which are strongly recurved, slender, and with the apices directed caudoproximally. Central projection corneous.

Allotypic Female.—Differs from the holotype in only a few minor details—epistome comparatively shorter and cephalomedian depression less well developed; opposable margin of immovable finger of chela with a row of eight tubercles, the third from base largest; that of dactyl with a row of 12 tubercles, the fourth from base largest as in holotype. (See measurements.)

Annulus ventralis (Fig. 12) subovate, broader than long, and with an elevated, rounded caudal wall; a rounded elevation extends from cephalosinistral margin caudodextrally to near the median line where its margin forms the cephalic wall of the inverted U-shaped sinus; the caudosinistral wall of the

elevation descends beneath the sinistral rim of a tongue-like prominence which, in turn, passes beneath the afore-mentioned oblique elevation, the separation between the two being marked by the sinus.

Morphotypic Male, Form II.—Differs from the holotype in possessing a rostrum, the acumen of which reaches cephalically only to base of distal joint of peduncle of antennule, and marginal spines reduced to corneous acute tubercles; lateral spines on carapace minute; opposable margin of immovable finger of chela with a row of 13 tubercles, the fourth from base largest; corresponding margin of dactyl with a row of 19 tubercles, the fifth from base largest; caudodextral angle of cephalic section of telson with three spines. (See measurements.)

First pleopod (Figs. 14, 15) extends to caudal margin of coxa of third pereiopods when abdomen is flexed. Two terminal elements strongly recurved at an angle slightly greater than 90 degrees to the main shaft of the appendage, and in contact except at distal extremity. Mesial process extends slightly beyond tip of central projection, and neither element corneous.

Measurements.—As follows (in millimeters):

		Holotype	Allotype	Morphotype
Carapace	— height	7.8	*	10.5
	width	10.7	*	12.5
	length	22.6	21.6	27.4
Areola	— length	9.3	9.1	12.3
	width	1.7	1.6	1.8
Rostrum	— length	4.6	4.4	5.1
	width	3.2	3.2	4.0
Chela	— length of inner margin of palm	8.2	7.2	9.6
	width of palm	6.6	5.3	7.2
	length of outer margin of hand	19.5	16.9	24.2
	length of dactyl	10.0	8.5	12.6

* Carapace flared, measurement not possible.

Type Locality.—Cave Spring Cave, 12.1 miles northwest of Valhermosa, Morgan County, Alabama. "Cave Spring Cave is a typical underground stream although there are some rooms scattered about here and there. That cave is 3,050 feet long, or longer, and the water is quite cold. At times the stream is muddy and completely fills many parts of the passage. In fact, one cannot go very far back into it in wet seasons. The crayfish fauna is rather abundant, and I could easily have taken a gallon of specimens. Cave Spring Cave, as does Shelta Cavern, has white fish." (W. B. Jones, as quoted by Rhoades, 1941:144.) The cave has developed in the Tuscumbia (Mississippian) limestone, and is inhabited by a large colony of bats (*Myotis grisescens* Howell). Earthworms, enchytraeids, spiders (*Nesticus* sp.), carabids (*Pseudanophthalmus lodingi* subsp.), *Asellus* sp., and millipedes (*Pseudotremia* sp.) are rather abundant. The stream is typical for large caves in flat-lying limestones — broad, shallow basins; deep, still pools; a few riffles over gravel bars. A major fork occurs about half a mile from the mouth, with two large passages continuing beyond the fork. Maximum water depth is from four to five feet, averaging about 12 to 18 inches.

Dispositions of Types.—The holotypic male, form I, and the allotypic female are deposited in the United States National Museum, and the morpho-

typic male, form II in the Tulane University Collection. Three female and one male paratype are in the latter collection, and two female paratypes in the collection of the senior author at the University of Virginia.

Range.—*C. jonesi* is known from only two localities, that cited above and Shelta Cavern, Huntsville, Madison County, Alabama. Although Rhoades' specimen (1941:148) from the latter locality has not been examined, Dr. George H. Penn, Jr., has kindly lent us two cambarids collected there by Dr. R. D. Suttkus on September 8, 1958, and both of them are females of *C. jonesi.* No other records for *C. hamulatus* have been recorded from this area, and it seems probable that Rhoades specimen was actually *C. jonesi.* The range of *C. hamulatus,* as pointed out above, is to the northeast.

Specimens Examined.—Type locality: May 2, 1959 (1 ♂ I, 3 ♀ ♀) T. C. B. and H. R. Steeves, coll.; October 19, 1957 (2 ♂ ♂ II, 1 ♀) R. D. Suttkus, coll. Shelta Cavern: September 8, 1958 (2 ♀ ♀) R. D. S., coll.

Relationships.—*Cambarus jonesi* has its closest affinities with the members of the Extraneus Group. That *C. extraneus, C. hamulatus,* and *C. jonesi* share a common ancestry that is not too remote was pointed out in the discussion above.

Cambarus hubrichti Hobbs
(Figs. 21-30)

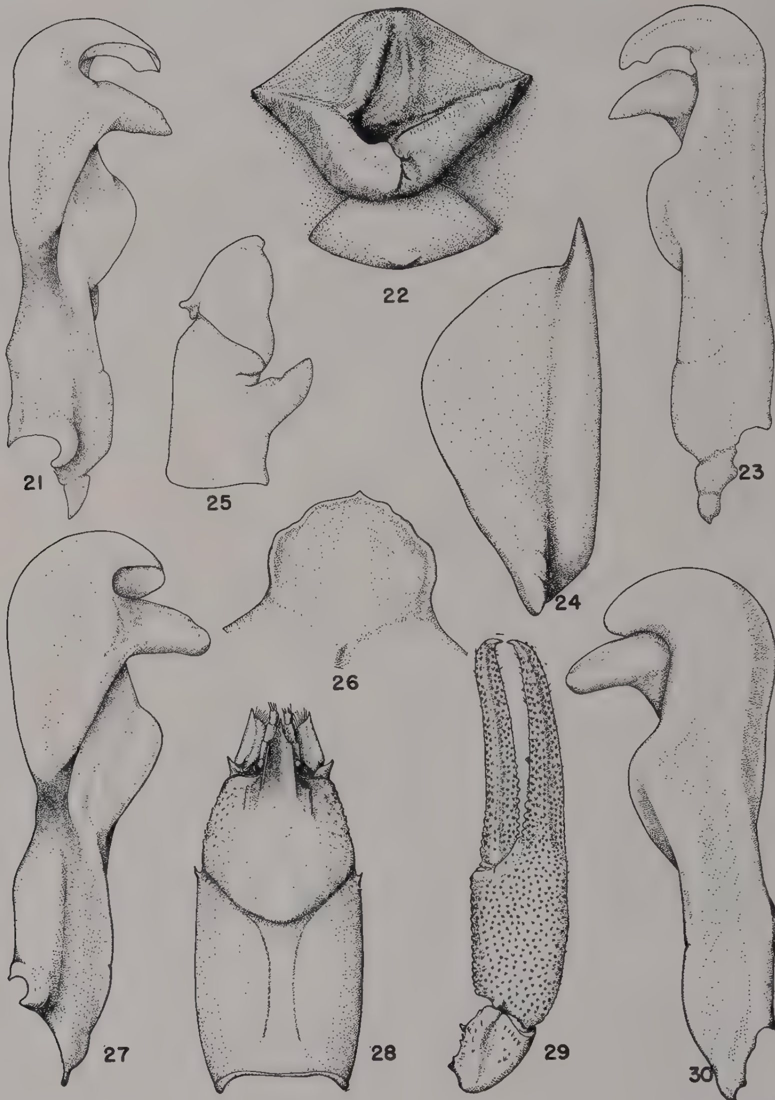
Cambarus sp. Hubricht 1950, Bull. Natl. Speleological Soc., 12: 17.
Cambarus hubrichti Hobbs 1952, Amer. Midl. Nat., 48 (3): 689-693, 8 figs. [Type locality: Lewis Cave, 15 mi. N.W. of Doniphan, Ripley County, Missouri — SW ¼ NE ¼, Sec. 30, T. 25N., R. 1E.] Wells 1957a: 639; Wells 1957b: 640; Wells 1959: 5, 7-9, 12-14.

Diagnosis. — Albinistic; eyes reduced; rostrum without lateral spines, sometimes with small corneous tubercles; sides of carapace with one to three spines on each side; areola about six times as long as broad and 41 to 44 percent of entire length of carapace with five punctations across narrowest part; antennal scale broad with distal margin of lamellar portion rounded; chelae not studded with conspicuously long setae; hooks on ischiopodites of third pereiopods; postorbital ridges terminating cephalad in spines. First pleopod of male and annulus ventralis of female as figured.

Range.—The range of *C. hubrichti* appears to be limited to the upper drainage of the Eleven Point and Current Rivers, at the eastern edge of the Ozark Plateau. It was collected from the type locality by Hubricht (1950) and Wells (1957). The latter also found this species in Dewey Minick Cave (NE ¼ SW ¼, Sec. 22, T. 25N., R. 4W.) Oregon County, and from Midco Cave (NE ¼ SW ¼, Sec. 27, T. 27N., R. 2W.) Carter County — both localities in Missouri.

Lewis Cave (type locality) is described by Bretz (1956:431) as large (up to 30 feet wide) and spacious for 850 feet from the entrance, then a low, wide stoopway, the stream with sand bars here, meandering across the passage. In the big part of the cave it runs "noisily" among the chert rubble. The mouth opens "at the foot of the valley slope of Big Barren Creek"; the point of exit of the stream is not known.

Midco Cave contains a stream which flows from a pond in the rear of the



Figs. 21-30.—*Cambarus hubrichti*. 21. Mesial view of first pleopod of male, form I; 22. Annulus ventralis; 23. Lateral view of first pleopod of male, form I; 24. Antennal scale; 25. Basipodite and ischiopodite of third pereiopod of male, form I; 26. Epistome; 27. Lateral view of first pleopod of male, form II; 28. Dorsal view of carapace; 29. Upper view of distal podomeres of cheliped of male, form II; 30. Lateral view of first pleopod of male, form II.

cave; below the pond the stream "flows over bed rock which it has faceted rather extensively and intensively." The stream floods occasionally as evidenced by driftwood in the back portions; when the floods occur, it flows out of the mouth of the cave but in normal times it finds some lower outlet. The cave opens at valley bottom level near Pike Creek (Bretz, 1956:294).

Remarks.—Wells (1959: 12) in studying the response to light by this species discovered that mature animals exhibit no response to "illumination of the cephalic region, tail or any other part of the body." "The one juvenile specimen [however] . . . showed marked photosensitivity." The lack of response of adults is contrasted with definite response exhibited by *C. setosus* when light is trained on its cephalic region (see below).

Dr. Wells has kindly permitted us to examine his specimens, and Figures 21, 23, and 25, illustrating the first pleopod and the hooks on the ischiopodite of the third pereiopod of the first form male, are based on his material.

Cambarus cahni Rhoades

(Figs. 31-37)

Cambarus cahni Rhoades 1941, Proc. U. S. Nat. Mus., 91 (3129): 146-148, 4 figs. [Type locality: Belgreen Cave, NW ¼ SW ¼ Sec. 12, T. 7S, R. 13W., Franklin County, Alabama.]

Cambarus cahni Hobbs 1942a: 354; Hobbs 1952: 689, 693.

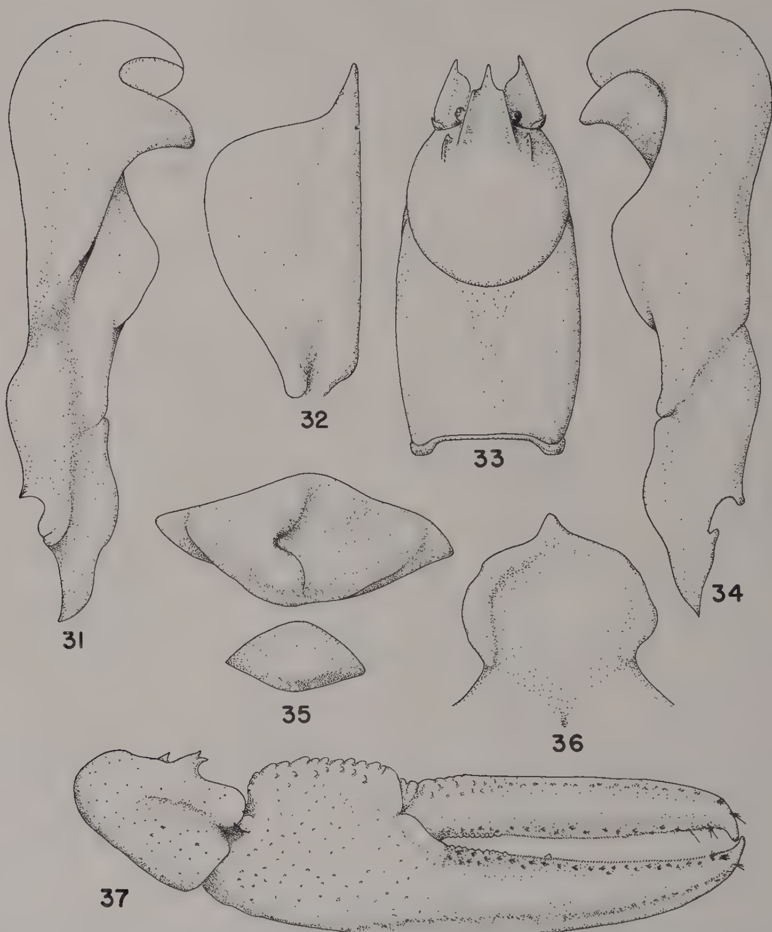
Diagnosis.—Albinistic; eyes reduced and with pigment; rostrum broadest at base with small lateral spines that are often reduced to angles; upper surface of rostrum with a broad median carina; postorbital ridges terminating cephalically in small tubercles; areola moderately broad, seven to eight times longer than broad and constituting 36.7 to 40.5 percent of the length of the carapace; a small tubercle present on each side of carapace; chela not conspicuously setose, relatively smooth, and with two or three rows of low tubercles on inner surface of palm; hooks on ischiopodites of third pereiopods in male. First pleopod of male and annulus ventralis of female as figured.

Range.—This species is known only from the type specimens. The type locality, "Belgreen Cave is a small cave with a very deep underground stream. The stream becomes muddy and almost fills the cavern in wet seasons" (Rhoades, loc. cit.:147).

As indicated, a crayfish that frequents several caves in northern Alabama and southern Tennessee is almost indistinguishable from *C. cahni* except that it is pigmented. Rhoades (loc. cit.:146) is probably referring to the same crayfish when he writes "I have a female crayfish from Sadler Spring Cave that is lightly pigmented on the carapace and dorsum of the abdomen. It bears close resemblance to *C. cahni* . . . but I do not place this record with *C. cahni*. . . ." A thorough study of more specimens of the pigmented form and of *C. cahni* must be made before their relationship can be established.

Cambarus setosus Faxon
(Figs. 38-47)

Cambarus setosus Faxon (in Garman) 1889, Bull. Mus. Comp. Zool., 17 (6): 237, 5 figs. [Type locality: Wilsons Cave, Jasper County, Missouri]. Faxon 1890: 621, 625, 628, 630; Parker 1890: 155-157, 161, 1 fig.; Lönnberg 1894b: 4, 5; Hay 1899: 959, 966; Ortmann 1902: 277; Hay 1902: 436; Steele 1902: 7, 16-18; Harris 1904: 59, 123-126, 134, 145, 153, 162;



Figs. 31-37.—*Cambarus cahni.* 31. Mesial view of first pleopod of holotypic male, form II; 32. Antennal scale of holotype; 33. Dorsal view of carapace of holotype; 34. Mesial view of first pleopod of holotype male, form II; 35. Annulus ventralis of allotype; 36. Epistome of holotype; 37. Upper view of distal podomeres of cheliped of holotypic male.

Ortmann 1905: 118, 120, 121, 127; Faxon 1914: 422; Ortmann 1931: 95; Creaser 1931: 6, 7; Creaser and Ortenburger 1933: 15, 16, 17, 22, 41, 1 fig.; Hobbs 1941: 114; Hobbs 1942b: 163; Burbanck, et al.: 1948: 360-367; Hubricht 1950: 17; Hobbs 1952: 689, 693; Williams 1954: 809, 901, 902-904, 914, 1 map, 8 figs.; Wells 1957a: 639; Wells 1957b: 640; Wells 1959: 3-12.

Cambarus ayersii Steele 1902, Pub. Univ. Cincinnati Bull., 2 (10): 7, 18-20, 50, Pl. VI, fig. 14. [Type locality: Fisher's Cave, near Springfield, Greene County, Missouri.] Faxon 1914: 422; Ortmann 1931: 95; Creaser 1931: 6-7; Creaser and Ortenburger 1933: 41; Hobbs 1941: 114; Hobbs 1942b: 163; Hubricht 1950: 17; Hobbs 1952: 689, 693; Williams 1954: 809, 902; Wells 1957a: 639; Wells 1957b: 640; Wells 1959: 3-12.

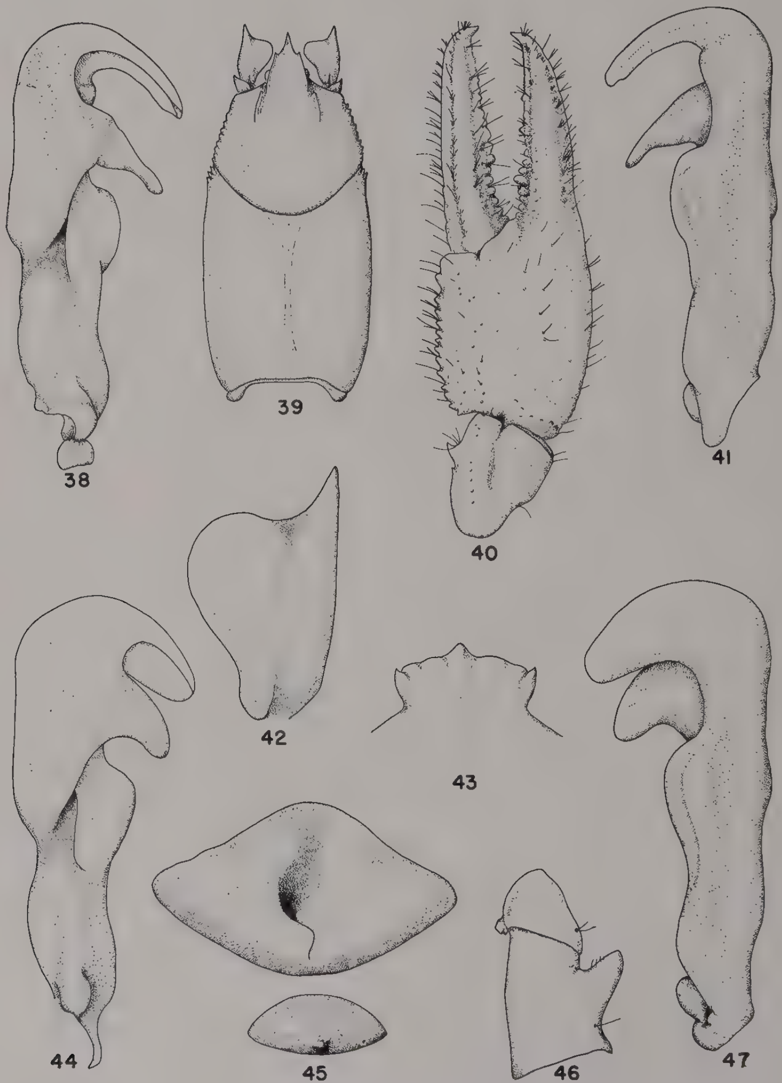
Diagnosis.—Albinistic, eyes reduced and without a pigment spot; rostrum broadest at base, with small lateral spines, frequently asymmetrically situated, and sometimes absent; postorbital ridges terminating cephalically with or without spines or tubercles; areola very narrow (more than 15 times longer than broad), often obliterated near midlength; one to several lateral spines on sides of carapace; chelae conspicuously setose and with a single well-defined row of tubercles along inner margin of palm. First pleopod of male and annulus ventralis of female as figured.

Range.—This species is known from definite localities only in the southwestern part of Missouri, principally in the James River drainage. Christian County: Smallins Cave, 7.4 mi. SE. of Galloway. Jasper County: Cave on Cool Brook, 7 mi. E. and .5 mi. N. of Carthage; cave on Cool Brook, 8 mi. E. of Carthage; Whisner Cave, 2 mi. NW, of Sarcoxie; Wilsons Cave, about 2 mi. NW. of Sarcoxie; well at Joplin. Greene County: Fishers Cave [now known as Sequiota Cave, in the Sequiota State Fish Hatchery in Galloway (see Williams 1954: 911)]. Burbanck, et al. (1948: 363) reported a "cave crayfish," presumably *C. setosus,* from "the mouth" of Wood Cave, about two miles from Smallins Cave. Three specimens, only one of which is mature, collected in northeastern Oklahoma (Cave between Spavinaw and Jay, Delaware Co., and Spring Creek, 5 mi. S. of Locust Grove, Mayes Co.) by A. P. Blair are tentatively assigned to this species; however, there are reasons to question this designation.

Smallins Cave (NW ¼ SW ¼, Sec. 12, T. 27N., R. 21W. in Christian Co., Mo.). This is a large stream cave in which the stream is perennially subject to "torrential floods." It is spacious for 600 feet beyond which it is necessary to wade in deep rimstone pools frequently floored with gravel (Bretz, 1956:298).

Apparently in earlier years *Cambarus setosus* was much more abundant than at present. Fairly good series collected two decades ago are available, but Dr. Oscar Hawksley (personal communication), of Central Missouri State College, has been in hundreds of the caves in the region with various biology students, and he has never seen a troglobitic crayfish in them.

Remarks.—We are following Williams (1954: 903) in considering *ayersii* to be a synonym of *setosus* for among series of specimens of the latter may be found all of the characteristics which are said to be those of *ayersii.* Williams (*loc. cit.*) states that his specimens were collected in caves in which "the water was clear and cold. Only one



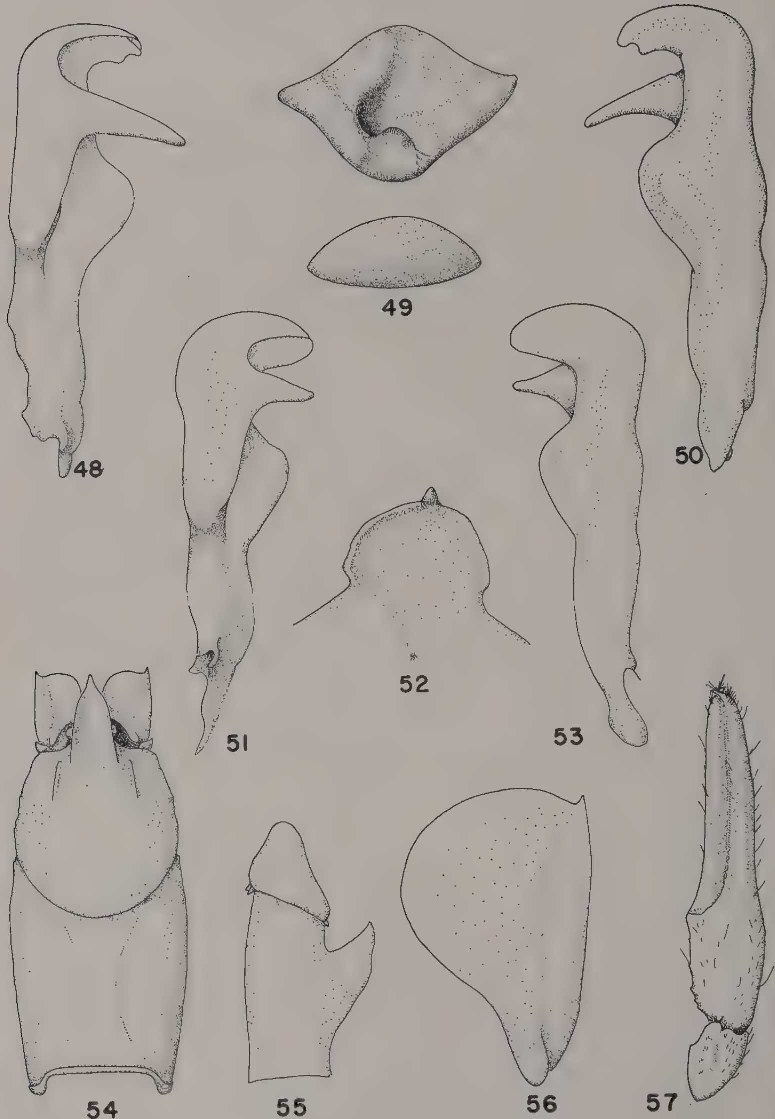
Figs. 38-47.—*Cambarus setosus*. 38. Mesial view of first pleopod of male, form I; 39. Dorsal view of carapace of male, form I; 40. Upper view of distal podomeres of cheliped of male, form I; 41. Lateral view of first pleopod of male, form I; 42. Antennal scale; 43. Epistome; 44. Mesial view of first pleopod of male, form II; 45. Annulus ventralis; 46. Basipodite and ischiopodite of third pereiopod of male, form I; 47. Lateral view of first pleopod of male, form II.

of these specimens has been taken in the twilight zone of a cave in the daytime and it was found under a rock. The rest of the collections have been made from pools in the region of total darkness in the daytime, or have been made near the entrance of a cave . . . at night. This is in opposition to the observations recorded by Faxon (1899: 227) who stated that *C. setosus* was active in wells and at the mouth of a cave in broad daylight.

"Crayfishes in the dark regions of the caves did not seem to be affected by the light of lanterns. Individuals were found resting in open water on the solid rock or mud bottom, and rarely were taken from under cover. All of the specimens were easily picked up by hand, but they swam feebly when disturbed. This again is in opposition to observations recorded by Faxon (1889: 227) who reported *C. setosus* as extremely difficult to capture even if the water was only slightly agitated."

Additional notes made by Mr. Robert T. Bray (personal communication) on specimens collected in Smallins Cave include the following observations. On April 24, 1949, he collected two specimens; one was taken from a pool about 235 yards from the entrance of the cave where "a faint glimmer of light can be seen from the entrance . . ." and this specimen was "neither white nor brown but a sort of mixture of the two. The second specimen was taken from a pool 20 inches deep, a few feet farther back than the first. No light from the entrance can be seen at this point. . . . The temperature of the water in these pools is 54°F. All the crayfish I observed were affected by the light and moved slowly for cover whenever my light was on them." In October, Mr. Bray sent two additional specimens to me with the accompanying notes. "Both these specimens were taken in the same pool, just eight feet farther back in the cave from that of last April. The temperature of the water here as well as at the entrance of the cave is 57°F., in contrast to the 54°F. recorded last April. So much surface water probably accounts for the three degree rise. Another noteworthy fact is that both these creatures were noticeably more sluggish than those of last spring; they presented no difficulty in capture while those before were quite active and temporarily eluded capture. These two specimens have considerably more pigment than those of before although the cave, at this point, is in perpetual darkness."

The apparent discrepancies in the observations made by Williams and those made by Miss Ruth Hoppin (reported by Faxon) are supported by Bray. It would be interesting to know whether or not these differing responses may be correlated with seasonal, diurnal or flooding conditions in the cave. The latter is suggested because of the probable lowered mineral content of the water during flooding, and it is at least possible that this might affect the crayfishes. It seems unlikely that the temperature differences observed by Bray are to be correlated with the response of the animals to being disturbed, for if



Figs. 48-57.—Cambarus cryptodytes. 48. Mesial view of first pleopod of male, form I; 49. Annulus ventralis; 50. Lateral view of first pleopod of male, form I; 51. Mesial view of first pleopod of male, form II; 52. Epistome; 53. Lateral view of first pleopod of male, form II; 54. Dorsal view of carapace of male, form I; 55. Basipodite and ischiopodite of third pereiopod of male, form I; 56. Antennal scale; 57. Upper view of distal podomeres of cheliped of male, form I.

any effect were produced one would expect the animals to be more active at the higher temperature.

Experimental data on response to light obtained by Wells (1959: 11-12) permitted the following conclusions. "*C. setosus* and *C. ayersii* [= *C. setosus*] were similar in their responses to light. All specimens examined were photosensitive. No differences in the response patterns were noted with crayfish of different sizes. No sex difference was observed. . . . A response could be measured only when the head of the animal was illuminated" but experiments indicated that the eyes, eyestalks, antennae and antennules do not act as receptors. Wells suggests that "possibly the cerebral ganglion is functioning directly as a photoreceptor in these cave crayfishes. . . . It is suggested that the long wave-length limit of sensitivity for *C. setosus* and *C. ayersii* is between λ 6600Å and λ 7300 Å in the red. The short wave-length limit of sensitivity has not been determined."

Burbanck, *et al.* (1948: 367) in testing the toleration of this species and *Cambarus rusticus* [probably *Orconectes neglectus neglectus* (Faxon, 1885b: 142)] found that "the cave and stream crayfish reduced the water to approximately the same oxygen tension — no significant difference between .1978 and .2452 respectively" although *C. setosus* lived longer, 829.9 ± 35.0 minutes as opposed to the stream form which lived only 272.3 ± 21.5 minutes. They concluded that the cave crayfish "seem to have a lower rate of metabolism than the stream crayfish."

Cambarus cryptodytes Hobbs
(Figs. 48-57)

Cambarus cryptodytes Hobbs 1941, Amer. Midl. Nat., 26 (1): 110-114, 11 figs. [Type locality: A well, two mi. S. of Graceville, Jackson Co., Florida on farm of Mr. R. W. Williams.] Hobbs 1942a: 354; Hobbs 1942b: 9, 12, 32, 156, 157, 158, 162-163, 171, 5 figs. Hobbs 1952: 689, 693.

Diagnosis.—Albinistic, eyes reduced and without pigment spot; rostrum broadest at base, margins tapering to tip and without marginal spines or tubercles; postorbital ridges terminating cephalically in small acute spines; areola broad, about four times as long as broad, and its length about 39 percent of entire length of carapace; a single small tubercle present on each side of carapace; chelae not conspicuously setose; male with hooks on ischiopodites of third pereiopods. First pleopod of male and annulus ventralis of female as figured.

Range.—This species is known only from the type locality (see above).

Remarks.—The seven known specimens of this species were taken from an open well about 60 feet in depth by Mr. R. W. Williams.

Acknowledgments.—We wish to express our sincere appreciation to the following persons who have contributed or lent us specimens which have been examined during the course of this study: Drs. Charles E. Mohr, Patrick H. Wells, George H. Penn, Jr., Fenner A. Chace, Jr., James N. Dent, Henry T. Kirby-Smith, Messrs. Leslie Hubricht, Robert T. Bray, and Byron C. Marshall.

We would also like to thank Messrs. Carl J. Freeman and Horton H. Hobbs III for assisting us in the preparation of the plates.

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Speciation Among Cave Opilionids of the United States[1]

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Introduction

The opilionids or phalangids are members of the Order Opiliones of the Class Arachnida. Other orders within this class include such abundant and well-known forms as the spiders, pseudoscorpions, scorpions, whip scorpions, mites, and a few lesser known groups. The opiliones are nearly world-wide in their distribution; they are found from the far North to southern areas such as Argentina and South Africa. Widespread and abundant as they are, they achieve their greatest variety and abundance in the tropical and subtropical regions of the world.

The opiliones are quite varied in appearance and size, but all have the following common characteristics:

1. An unsegmented cephalothorax which is broadly joined to the faintly segmented abdomen.
2. Three-segmented chelate chelicerae.
3. Six-segmented palpi.
4. A pair of simple eyes which are usually located on a tubercle on the anterior third of the cephalothorax.
5. A genital opening on the second abdominal segment, usually covered by a genital plate.
6. A pair of scent glands at the anterior part of the cephalothorax.
7. Respiration by means of tracheae with spiracles located on the second abdominal segment.

Within the order Opiliones, there are three suborders as follows:

I. Cyphophthalmi: mite-like forms. Species are known from the states of Washington and Florida, without known species between. No cave forms are known in the United States.

II. Laniatores: tropical and subtropical forms, with but a few exceptions. There are a number of Laniatores in the southeastern United States and a few in the West. Species occur along the west coast as far north as central British Columbia. Some of the Laniatores have brightly colored bodies with elaborate dorsal color patterns as well as spines and tubercles. Usually they are found in moist areas, living under rotten logs or under stones. In tropical rain forests, some

[1] These studies on opilionids were supported in part by a grant from the National Science Foundation.

are found in the bromeliad clumps high up in trees. Since many of the Laniatores are small and live in dark places, they often inhabit caves. It is among the members of this suborder that the largest number of cavernicoles are found. In the United States and Mexico, three families are represented: (1) Cosmetidae; (2) Phalangodidae; and (3) Triaenonychidae.

Another family, the Gonyleptidae, is found in Central and South America. Neither the cosmetids nor the gonyleptids have representatives that seem to be true cave forms. The family Phalangodidae has the greater number of cavernicoles, but in the New World only one true cave form is known among the Triaenonychidae.

III. Palpatores. These are the commonest opilionids of this country. Two subgroups are recognized:

1. Dyspnoi: small secretive forms found in leaf mold. Among this group, a few true cavernicoles have evolved.

2. Eupnoi: the common long-legged species found all over the world. Most belong to the family Phalangiidae. These include the long-legged daddy-long-legs with which everyone is familiar. They are particularly common in the late summer and early fall. While frequently encountered in caves, no true cavernicoles are known.

CAVE ADAPTATIONS

Opilionids have a number of structural adaptations to cave life, many of which are quite obvious. One of these adaptations is the reduction or even complete loss of the eyes. Among some cave forms, an eye tubercle is present, but no eyes are visible externally. Among others, the eyes are present but the retina does not have the characteristic black color and appears to be nonfunctional. All degrees of development in this direction can be found.

Another development is the increased length of legs. Cavernicolous species tend to have longer and less robust legs than their epigeic relatives (Table I). Color, too, is another adaptation. Among the phalangodids living outside caves, the body color is usually bright

TABLE I.—Comparative measurements of a cavernicolous and an epigeic form of *Crosbyella* sp.

Length of legs	Epigeic form	Cavernicolous form
I.	2.9 mm	6.6 mm
II.	4.2 mm	11.1 mm
III.	3.3 mm	9.1 mm
IV.	4.4 mm	10.6 mm
Length of palpus	2.1 mm	2.8 mm
Total length of body	1.9 mm	2.0 mm
Length of cephalothorax	0.6 mm	0.6 mm
Width of body	1.4 mm	1.6 mm

reddish brown. In partially adapted types, the color is lighter and in true cavernicoles the color may be absent and the animal white. Associated with color is the degree of sclerotization. The cave species are much more weakly sclerotized than their epigeic relatives.

The true cavernicoles that have been described from the United States show no tendency towards an increase in size (Table I). Among some species known from Mexican caves, however, there seems to be this tendency. Some species described from caves in Mexico are many times larger than any related epigeic species.

Little is known of the physiological adjustments of these cave animals, but from their structure and habits it appears that they are more susceptible to drying than epigeic species. They would undoubtedly be less tolerant of changing conditions in their environment than related species living outside the caves. Much research remains to be done on the ecology, physiology, and habits of these cave forms.

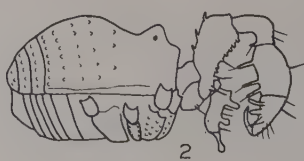
Distribution of the Cave Species

By far, the largest number of cave species occur in the southeastern states.

Phalangodes armata Tellkampf is a true cave species, fully differentiated from its epigeic relatives (Fig. 1). It was first described from Mammoth Cave, Kentucky, and is now known from many caves in Kentucky and Tennessee. The specimens from Tennessee have a greater number of tarsal segments and were first thought to be a distinct species. Further collections have shown that transitional forms exist.

Phalangodes brunnea Banks is a strictly epigeic species which is known from a wide area encompassing Tennessee, the Great Smoky Mountain country, Georgia and Alabama (Fig. 2). It has been known to enter caves, but no strictly cave-adapted forms have been discovered.

Bishopella laciniosa (Crosby and Bishop) is widely distributed in and out of caves of the southern part of the Ohio River Valley region. It is frequently encountered in caves. Many show no cave adaptations, others show varying degrees. One specimen from a cave in Mt. Eagle, Tennessee, has long legs, a lighter color, and reduced eyes.



Figs. 1 and 2.—A comparison of two related species. 1. *Phalangodes armata,* a cavernicolous form; 2. *Phalangodes brunnea,* an epigeic form.

While it is not considered a true troglodyte, it certainly has some of the characteristics of such forms.

Phalangodes flavescens (Cope) is also found in a number of localities north of the Ohio River. It is primarily an epigeic form. In those caves where it has been found, such as in Virginia and the type locality, Wyandotte Cave in southern Indiana, it is lighter in color, has reduced eyes, and possesses somewhat longer legs. The individuals of a large population were once observed in Wyandotte Cave. They were feeding upon fungi which were growing on wood and the specimens showed many adaptations for cave living.

The southern portion of the Ohio River region is dominated by *Bishopella laciniosa;* north of the Ohio River, only the cave-adapted *Phalangodes flavescens* is found.

Phalangodes armata (Cope) is found south of the Ohio River, but occupies the middle portion of central Kentucky and Tennessee.

All the cavernicolous species are presumably derived from modern epigeic forms which can be found in localities both inside and outside the caves.

Other species, such as *Crosbyella* sp. in Arkansas, also have populations and races that are adapted to the cave environment.

Among the Palpatores, there are also cavernicolous forms. *Nemastoma inops* Packard has been reported from Kentucky caves and *Nemastoma pallidimaculosa* Goodnight and Goodnight was described from Rock House Cave near Oleander, Alabama. These are true cave species. Other epigeic species of this same genus live in leaf mold.

In the western states, only a few cavernicoles have been discovered. As the types of opilionids that readily differentiate into cave forms are not abundant in the dry areas that are found throughout the West, that is quite understandable. One member of the genus *Nemastoma* (*N. packardi* Roewer) is reported from a cave in Utah. Three widely scattered species of Laniatores are known from caves, and further exploration may yield more. These are:

Texella mulaiki Goodnight and Goodnight from Hays County, Texas.

Phalangodes californica (Banks) from Alabaster Cave, California.

Sclerobunus cavicolens (Banks) from Morrison's Cave near Bozeman, Montana.

DISCUSSION

The reasons for the development of some species of opilionids into cavernicolous forms can be speculated upon, but certainly at this time not determined. There must be some genetic factor which determines the direction of mutations. The long-legged leiobunums often congregate in large numbers in dark, moist places, so they are encountered in caves, usually not far from the entrance. They cluster in great clumps from the ceiling or walls of the cave. In spite of this predilection for caves, no true cavernicoles have evolved among the leiobunums and they are seldom, if ever, found deep within the

caves. Cosmetids too, for the same reason, often inhabit the favorable environment found in caves. In Mexico where this group is abundant, large numbers of cosmetids may be collected in moist caves, but they too seem generally unable to develop into true cavernicoles.

It is among the phalangodids that the greatest plasticity in the direction of mutations leading to a true cave existence are found. It is within this group that species that are truly cavernicoles exist. Some live deeply within caves and are so well adjusted to it that they could not survive outside such a constant environment. In this group are species closely related to epigeic forms that are outside the cave in the damp leaf mold of surrounding areas. In fact, among some groups of species, it is possible to observe the transition from the epigeic species to the cavernicolous species. These often have intermediate forms near the cave entrance with the true cavernicolous forms deep within the cave.

CONCLUSION

In conclusion, it can be said that in those groups that are genetically plastic, many cave forms have evolved. Usually their relationship with an epigeic species can be demonstrated. A review such as this points up how much remains to be learned concerning cave forms. Many caves, especially in the West, remain to be explored. Practically nothing is known of the embryology, life history, ecology, or physiology of cave opilionids.

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A Preliminary Survey of the Knowledge of North American Cave Collembola[1]

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At the present time virtually nothing has been published concerning the cave collembolans of North America. As simple proof of this, a bibliography of North American cave Collembola contains less than 30 entries, most of which are antiquated or mere listings of one or two erroneously identified species in a cave fauna of Blank Cave. The only general survey is that of Packard (1888) which encompassed less than one percent of the actual fauna and, from a taxonomic viewpoint, is either useless or seriously damaging. In addition to the work of Packard, various forms were described by Banks (1897). The accuracy of these descriptions can be measured if we consider that they were made generally with the use of a hand lens upon specimens often less than a millimeter in total size. The only adequate works devoted solely to North American cave forms are those of Denis (1929) upon Oregon material collected by Silvestri, of Delamare Deboutteville (1949) upon material from a few caves in Alabama and Tennessee collected by Henrot, and of Bonet (1934) upon material largely from a few Kentucky and Virginia caves. All of these works were published in European journals and are in French. In addition, several authors (Mills 1934, 1948, Bonet 1943, Wray 1952, and Christiansen 1958) have described single cave species from the United States in larger works concerned with other groupings. It is not possible to obtain a view of the cave Collembola fauna of the United States from this bibliography; however, work now in press, or in progress, will greatly increase our records in the genera *Sinella* (Christiansen, 1960) and *Pseudosinella* (in preparation). Much of the cave area of the United States is still virtually untouched from the standpoint of collembolans, and experience has shown that the simple statement that "no collembola occur" is no indication of the presence or absence of these animals. In personal experience Collembola have been found in about two-thirds of the caves previously indicated to have none. Even the most astute collector may pass up these minute forms without experience and exhaustive search, or use of berlese extraction. At the present moment only the southeastern quadrant of the country has relatively complete collections, but examination of these, combined with the spotty collections from other parts of the country permits a rough guess as to the probable composition of the fauna. The following genera are known to occur in American caves

[1] Much of the work on this paper was made possible by a National Science Foundation Grant, G-4563.

and have probable or actual troglobitic species: 1) *Arrhopalites;* 2) *Entomobrya;* 3) *Folsomia;* 4) *Hypogastrura;* 5) *Lepidocyrtus;* 6) ***Megalothorax;* 7) *Oncopodura;* 8) *Onychirus;* 9) ***Pararrhopalites;* 10) **Parasinella;* 11) *Pseudosinella;* 12) *Sinella;* 13) *Tomocerus;* 14) *Tritomurus;* 15) **Troglosinella;* and 16) ***Tullbergia.* In addition to this group, several genera seem to be likely candidates for inclusion in the list (i.e., *Heteromuris* and *Troglopedetes*) but have not as yet been found here, while a number of other genera of cave collembolans, found in Mexican caves (ex. *Mesogastrura*) may be yet uncovered in caves of the west or southwest. In addition, there is always the strong possibility of turning up entirely undescribed genera in North American caves.

The remainder of this paper will be devoted to a brief discussion of the sixteen genera listed above, their presently described cave forms and the possible nature of the total fauna as indicated in preliminary examinations of extant collections.

SUBORDER SYMPHOPLEONA

Only three genera of this suborder have been found so far in United States caves: *Arrhopalites* and *Pararrhopalites* of the family Sminthuridae and *Megalothorax* of the family Neelidae. It is quite likely that more genera of the last family will be discovered with exhaustive search.

Arrhopalites

This is the most widespread and common genus of the suborder in caves, and two cave species have been described:

Arrhopalites ferrugineus (Packard) new combination
Syn.: *Smynthurus ferrugineus* Packard 1888

Arrhopalites mammouthia (Banks) new combination
Syn.: *Smynthurus mammouthia* Banks 1897

It is quite possible that both the species mentioned above are synonyms of a widespread epigean species, but it appears likely that a few strictly cave forms have evolved in the group. The genus is found in most cave systems but there are relatively few species concerned.

Pararrhopalites

At least one species of this genus has been found in a cave, and it is possible that several species occur scattered through western cave areas.

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* Genera synonymized in works now in press or preparation.
** These forms have not been recorded previously in U. S. caves.

Megalothorax

One species has been found from a western cave, and undoubtedly more of this genus and related genera (*Neelus, Neelides*) will be turned up with diligent collection. The extremely minute size of these animals combined with their abundance in deep soil layers makes it unlikely that many troglobite species will be found in the near future.

SUBORDER ARTHROPLEONA
FAMILY ENTOMOBRYIDAE

Entomobrya

A single troglobitic species has been described from a cave in South Dakota. Comparison with European records makes it appear unlikely that many more cave species will turn up, or that the described species (*E. troglodytes*) is widespread.

Sinella

Two cave species, *Sinella cavernarum* Packard 1888 and *Sinella hoffmani* Wray 1952, have been described, and in a paper now in press (Christiansen, 1960) five additional species are described. The genus is largely confined to the southeastern quadrant of the United States and only one species (*S. cavernarum*) is found in areas around the borders of this region. The seven species described probably represent almost the whole fauna in this country.

Parasinella

This is synonymized with *Sinella* in the work mentioned above.

Pseudosinella and *Troglosinella*

Work in progress indicates that these two genera are also synonyms. There appear to be about seven troglobitic species (two already described) also primarily confined to the southeastern quadrant of the country. The limits of this genus are somewhat broader than those of *Sinella* and a few species may occur in as yet unexplored western caves. It is doubtful that any extensive speciation has occurred.

Lepidocyrtus

A single species, *L. atropurpureus*, has been described by Packard (1888). Examination of the animals will probably show them to be a troglophilic *Pseudosinella*. It is doubtful that any troglobitic species of this genus exist in the United States.

Tomocerus

Two cave species of the genus have been described. The first, *T. pallidus* Packard, is probably a synonym of the troglophile, *T. flavescens,* but extensive topotypic collections will have to be examined to determine this. The second species, *T. brevimucronata,* appears to be a troglobite. The fact that *Tomocerus* is one of the commonest genera in caves throughout the United States makes it quite likely that a few more troglobitic species will be uncovered.

Tritomuris

This is the cave genus having the most species (four) of any in the United States. It is well represented in all parts of the country and, while not nearly as ubiquitous as the genus *Tomocerus,* and many new troglobitic species will undoubtedly be uncovered, particularly from the west.

FAMILY ONCOPODURIDAE

Oncopodura

O. cruciata Bonet 1943 has been described from caves in Montana and a second species has been found in midwestern caves. The genus appears to be confined to caves west of the Mississippi. Further work may show several endemic species in this area.

FAMILY ISOTOMIDAE

A number of troglophilic or trogloxenic species have been found in genera belonging to this family (*Folsomides, Isotoma,* etc.), and one or more of these may have locally evolved troglobitic species. Present evidence indicates that only *Folsomia* is likely to have produced many such species.

Folsomia

Only one species belonging to this genus has been described from North American caves.

Folsomia cavicola (Banks) new combination
Syn.: *Entomobrya cavicola* Banks 1897

In addition, several other species of the genus have been seen in caves, and it is most likely that some of these at least represent troglobites. Most of the species so far seen are found in southeastern caves.

FAMILY HYPOGASTRURIDAE

It is quite probable that several of the Mexican genera of cave forms in this family occur in the southwest, but at the moment only a single species has been described.

Hypogastrura

The only troglobitic species of the family known in the United States was described from Indiana.

Hypogastrura lucifuga (Packard) new combination
Syn.: *Lipura lucifugus* Packard 1888

This probably represents a local development. The genus is not widely represented in caves of the United States.

FAMILY ONYCHIURIDAE

Onychiurus

A single species (*O. obesus* Mills) has been described from caves of the United States. However, collections now at hand indicate that this genus will contain the bulk of North American troglobitic species. The genus is ubiquitous but is best represented in the western and northern parts of the country. It is probable that many collections represent local edaphic species which have invaded caves, but preliminary examinations have shown that some, at least, represent troglobitic species.

Tullbergia

No troglobitic species of this genus have as yet been uncovered; however, since members of the genus are widespread in caves, possibly some local speciation has occurred.

In conclusion, only one thing is certain — most of the cave Collembola of the United States are as yet undescribed. It is not possible, with present tentative examinations and incomplete collections, to determine definitely even the outlines of the fauna, but it appears that the western and southeastern areas have quite different faunas with different dominant genera. At the present moment it appears that the cave Collembola fauna of the United States will match that of Europe, both in size and variety of elements.

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The Cavernicolous Beetles of the Subgenus Rhadine, Genus Agonum (Coleoptera: Carabidae)

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The carabid beetles of the subgenus *Rhadine* Leconte are an interesting series of slender, depressed, wingless *Agonum* which are distinguished by their elongate appendages, strongly oblique humeri, and the absence of normal pigmentation; all known species are uniformly testaceous, rufotestaceous, or dark ferrugineous. In the majority of species the third antennal joint is longer than the fourth, although this character is often allometric, the third joint being proportionately much longer in larger species and individuals than in smaller ones. In many species, but not all, the elytral apices are produced and dehiscent to a greater or lesser degree. A lateral series of setiferous elytral punctures, three or four in the margin below the humerus and a variable number (range about 10 to 15) on the 8th interstria or in the 8th stria, is usually well-developed. The scutellar and apical elytral punctures are setiferous. The first three tarsomeres typically bear lateral grooves. The undersides of the legs are, in most *Rhadine,* sharply flattened from base to apex, the edges rectangular and parallel. Species referable to *Rhadine* range from southern Canada to the northcentral plateau region of Mexico and east to Maryland and the coastal plain of Alabama, but the known species are most numerous in the southwestern United States, especially Arizona, New Mexico, and Texas. They are most common under rotting logs and rocks in moist situations (especially at high altitudes), in the burrows of mammals, and in caves.

The cavernicolous habit has been reported for *A.* (*Rhadine*) *longicolle* (Benedict), known only from Carlsbad Caverns, New Mexico; for *A.* (*Rhadine*) *ozarkense* (Sanderson and Miller), known from a single Arkansas cave; for *A.* (*Rhadine*) *caudatum* (Leconte), known from numerous localities in the eastern United States; and for one troglophile and three troglobitic species in Texas (Barr and Lawrence 1960). Three new troglophile and three new troglobitic species are described in the present paper.

Acknowledgments.—The writer expresses his appreciation to the following persons and their respective institutions for loan of specimens: O. L. Cartwright, U. S. National Museum; Henry Dietrich, Department of Entomology, Cornell University; Ralph Ewers, Cincinnati Museum of Natural History; Henry F. Howden, Canada Department of Agriculture; Milton W. Sanderson, Illinois State Natural History Survey Division; and J. M. Valentine, Alabama Museum of Natural History. A special debt of gratitude is due those persons who assisted me in collecting the cave specimens: Royce Ballinger, Andrews, Texas; Arthur Hewitt and Paul Spangler, Carlsbad Caverns National Park;

H. Marvin Koepke, Edinburg, Texas; Bill C. Stewart, Cookeville, Tennessee; Mills Tandy, Ozona, Texas; and Donald Widener, Dallas, Texas.

The following abbreviations are employed throughout this paper: ANT 4/3—ratio of length of 4th antennal segment to length of 3rd segment; EL—length of elytra; EW—width of elytra; HL—length of head from anterior margin of labrum to apex of pronotum; HW—head width; M—arithmetic mean; N—number of specimens in the sample; PL—pronotum length; PW—pronotum width; R—observed range of the sample; S.D.—standard deviation of the mean; TL—total length, in millimeters; V—coefficient of variation. All lengths were measured along the midline; all widths are maximum widths. Aedeagi were cleared and mounted in polyvinyl-lactophenol. Aedeagal length was measured as the chord of an arc. An ocular micrometer was used for all measurements.

KEY TO SPECIES OF CAVERNICOLOUS RHADINE FROM THE UNITED STATES

1. Eyes well-developed, facets present 2
1.′ Microphthalmous cave species without facets in eye 8
2. Pronotum as wide as or wider than long 3
2.′ Pronotum longer than wide 4
3. Alternate elytral intervals with rows of setiferous punctures; Md.-Ill., south to Ala. .... *caudatum* (LeConte)
3.′ Elytral intervals without rows of punctures; hind angles of pronotum rectangular, strongly reflexed; south Alabama .... *jonesi* n. sp.
4. Six to eight irregularly placed setiferous punctures on basal ¼ of elytral disc; northwest Arkansas .... *ozarkense* (Sanderson and Miller)
4.′ No such discal punctures (except scutellar) on basal ¼ of elytral disc 5
5. Elytral apices acute, dehiscent; pronotum with 2 pairs of marginal setae 6
5.′ Elytral apices rounded; pronotum with anterior pair of marginal setae only; Eddy Co., New Mexico .... *longicolle* (Benedict)
6. Pronotum widest at the middle, behind anterior pair of marginal setae 7
6.′ Pronotum widest in apical 1/6, at level of anterior pair of marginal setae; Texas Panhandle to SE. Colorado .... *rubrum* n. sp.
7. Elytra strongly convex, longitudinal striation obsolete in darker, more fully sclerotized specimens; eyes 1/5 of a head length; form larger, more robust; Edwards, Kerr, Uvalde, and Val Verde Cos., Texas .... *howdeni* Barr and Lawrence
7.′ Elytra depressed, longitudinal striae shallow but always distinct; eyes 1/6 of a head length; form smaller, more slender; Edwards, Sutton, Pecos Cos., Texas .... *babcocki* n. sp.
8. Last palpal segments fusiform, not produced 9
8.′ Last palpal segments apically produced and rounded, somewhat swollen. (Fig. 3 D,E,F) 12
9. Last palpal segments finely truncate (Fig. 3 A,B) 10
9.′ Last palpal segments apically rounded (Fig. 3C); antennal segments III and IV subequal; Kendall Co., Texas .... *koepkei* n. sp.
10. Elytral striation obsolete; pubescence sparse; margin of pronotum sinuate near base only; aedeagus 1.01-1.23 mm long 11

10.′ Elytral striae feebly but always distinct; pubescence well developed; margin of pronotum sinuate in apical 1/3 and also near base; aedeagus 0.91-0.93 mm long .... *tenebrosum* n. sp.

11. Pronotum averaging 6/10 as wide as long; elytra proportionately shorter and wider; total length less (6.6-8.2, mean 7.2 mm); Bexar Co., Texas .... *infernale infernale* Barr and Lawrence

11.′ Pronotum averaging 7/10 as wide as long; elytra proportionately longer and narrower; total length greater (7.6-8.8, mean 8.0 mm); Bexar Co., Texas .... *infernale ewersi* n. subsp.

12. Eye diameter 3-5% of head length; pronotum with 2 pairs of marginal setae 13

12.′ Eyes about 0.025 mm; no marginal setae on pronotum; Travis and Williamson Cos., Texas .... *subterraneum* (Van Dyke)

13. Pronotum widest at middle; head not sharply convergent and narrowed behind eyes; aedeagus 0.93 mm (holotype) long; head, pronotum, and elytra wider; Kendall Co., Texas.. *specum* n. sp.

13.′ Pronotum widest in basal 1/3; head sharply convergent and narrowed behind eyes, attached to prothorax by a subglobular condyle; aedeagus 0.71-0.74 mm long; head, pronotum, and elytra narrower; Bexar Co., Texas .... *exile* Barr and Lawrence

1. *Agonum* (*Rhadine*) *caudatum* (Leconte)
Fig. 2A

Platynus caudatus LeConte 1863: 7. (Type: Mus. Comp. Zool., Harvard).
Agonum (*Rhadine*) *caudatum,* Csiki 1931: 848.

Length 12-15 mm. Elongate, slender, shining. Color when fully sclerotized dark ferrugineous, with a faint purple cast. Easily distinguished from all other *Rhadine* by the large size; the long, produced, dehiscent elytral apices; and the rows of setiferous punctures on alternate elytral intervals. These punctures are especially diagnostic. The pronotum length and width are subequal; the hind angles are rounded in most specimens, subquadrate and blunt in occasional southern specimens; the margin is strongly reflexed. Aedeagus very large (about 2.5 mm), elongate, the apex attenuate, bluntly rounded; vas deferens with proximal and distal patches of long, pointed scales; internal sac with very small, blunt scales.

This species has a wide range; I have seen specimens from Maryland, the District of Columbia, Virginia, Pennsylvania, Ohio, Illinois, Tennessee, and Alabama. It has been collected in a cave in southwestern Virginia (Bolívar and Jeannel 1931), from caves in northern Alabama (W. B. Jones, J. M. Valentine, Harrison Steeves, pers. comm.), and by me in six caves in central Tennessee.

A permanent colony inhabits a limited area of Cumberland Caverns, Warren Co., Tennessee, 250 to 500 feet from the Historic Entrance. Both callows and adults are found at all seasons of the year in this cave beneath large, flat stones in a sandy-floored gallery or abroad near the edges of intermittent pools. A few *Pseudanophthalmus* (*P. macradei* Val., *P. t. templetoni* Val.) occur nearby, but are more common in adjacent, damper parts of the cave. Remnants of

burrows may be observed beneath the stones, presumably excavated by the *Rhadine*. Captive *A. caudatum* from Cumberland Caverns were maintained for two months in a glass container floored with moist sand, feeding readily on hamburger. Most of the specimens congregated beneath a metal bottle cap placed on top of the sand, but two or three crowded into a small burrow dug by one of the beetles. In digging, the beetle worked beneath the surface head first, throwing the sand out with the hind legs.

2. **Agonum** *(Rhadine)* **jonesi** n. sp.
Fig. 2B

Type series.—Holotype male (Alabama Museum of Natural History, Tuscaloosa), allotype female, and five paratypes, Turk's Cave, near Brooklyn, Conecuh Co., Alabama, October 2, 1952 (Walter B. Jones). Paratypes in U. S. Nat. Museum and the writer's collection.

Diagnosis.—Closely related to *A. caudatum* (Lec.), differing in the sharper, more widely reflexed, rectangular hind angles of the pronotum; the smoother, more brilliantly shining elytral surface, without interstrial rows of setiferous punctures; the shorter elytral apices; and the smaller size and sharper apex of the aedeagus.

Holotype.—TL 12.5, HL 2.48, HW 1.89, PL 2.24, PW 2.71, EL 7.29, EW 4.36.

Turk's Cave Sample of A. jonesi n. sp. (N = 7)

	R	M	S.D.	V(%)
TL	11.7-13.4	12.5	0.5	4.1
HW/HL	0.73-0.80	0.76	0.02	3.1
PW/PL	1.11-1.21	1.17	0.03	2.7
EW/EL	0.54-0.58	0.56	0.01	2.3
PL/HL	0.86-1.00	0.91	0.05	5.2
EL/PL	3.35-3.61	3.45	0.10	3.0
ANT 4/3	0.65-0.76	0.71	0.03	3.8

Description.—Length 11.7-13.4 mm. Elongate slender, rufotestaceous to dark ferrugineous, polished, shining. *Head:* Rounded, 3/4 as wide as long, widest across the eyes; surface shining, microgranulate, glabrous; labrum gently emarginate (doubly or singly), twice as wide as long; frontal grooves shallow, abbreviate; antennal ridge weak, extending to anterior angle of eye; diameter of eye 1/3 a head length, eyes large, convex, prominent. *Pronotum:* Transverse, 1/10 to 1/5 wider than long, shining, finely microgranulate, glabrous; margin broadly and strongly reflexed from apex to base; anterior angles prominent, rounded; posterior angles large, rectangular, sharply reflexed; base rather deeply emarginate. *Elytra:* A little more than half as wide as long, brightly shining, slightly iridescent, microalutaceous, glabrous; intervals very flat, striae feebly impressed; three discal punctures on 3rd interval; 17-19 marginal punctures with setae of variable length; widest in basal 1/3, evenly tapering to apical sinus in apical 1/11. *Appendages:* Terminal palpal segments finely

and sparsely pubescent, tips barely truncate, not sharply so; mandibles large and porrect. Antennae reaching middle of elytra when laid back; segment IV 7/10 as long as III; heavy pubescence beginning on apical half of IV. Legs long and slender, normal for the subgenus; tarsal segments with both lateral and dorsal grooves. Aedeagus 3/4 as long as that of *caudatum* (1.79 mm in paratype *jonesi*); apex of medium lobe sharply attenuate; internal sac with small, blunt scales; vas deferens with patches of long slender scales.

Remarks—It is a great pleasure to name this species in honor of its discoverer, Dr. Walter B. Jones, State Geologist of Alabama and Director of the Alabama Museum of Natural History, whose enthusiastic interest in beetles and cave fauna has resulted in the capture of many new and unusual species of cavernicoles.

3. **Agonum** *(Rhadine)* **ozarkense** (Sanderson and Miller) new comb.

Rhadine ozarkensis Sanderson and Miller 1941: 39. (Type· Illinois St. Nat. Hist. Surv. Div. coll., Urbana).

Closely similar in color (dark ferrugineous with faint purple cast) and general appearance to *A. caudatum* (Lec.), differing principally in the cordate pronotum (PW/PL about 8/10), the limitation of setiferous punctures on the intervals to the basal region of the elytra, and the smaller aedeagus (3/4 as long as that of *caudatum*).

Holotype male.—TL 11.7, HL 2.39, HW 1.56, PL 2.44, PW 2.02, EL 6.58, EW 3.54, ANT 4/3 0.80, aedeagus 1.79.

Length about 12-14.5 mm, width 3.5-4 mm (Sanderson and Miller, 1941). Head 13/20 as wide as long; eye diameter 1/5 to 1/4 of a head length. Pronotum with apex and base subequal, 6/10 the maximum width, which is in apical 4/10; margin narrowly reflexed, evenly arcuate, slightly sinuate before base; hind angles right, rounded, not produced; two pairs of marginal setae. Elytra with 6-8 rather long discal setae irregularly placed in basal 1/4; marginal punctures 18-19; microsculpture granulate, isodiametric, more intense than in *caudatum* but not coarser; surface dull shining (shining in *caudatum* and *jonesi*). Palps fusiform, truncate at the tips; pubescence beginning on apical 2/3 of antennal segment IV; segment IV 8/10 as long as III; tarsi with lateral and dorsal grooves. Aedeagus about as in *jonesi,* with similar distribution of long scales on vas deferens, in proximal and distal patches.

This species is known only from the type series of five specimens, trapped in the winter of 1939-1940 in Fincher's Cave, near Fayetteville, Washington Co., Arkansas.

4. **Agonum** *(Rhadine)* **rubrum** n. sp.

Type series.—Holotype male (U. S. Nat. Mus.), allotype female, and 3 paratypes, Big Mouth Cave, 3 mi. N. of Shamrock on left bank Red River, Wheeler

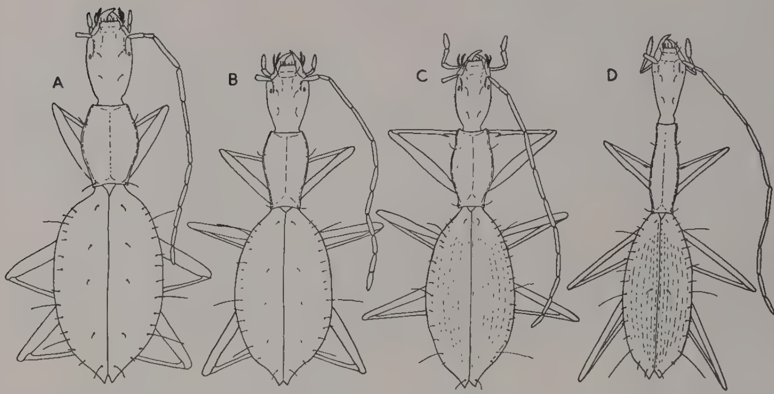

Fig. 1.—A. *Agonum (Rhadine) infernale ewersi* n. subsp. B. *Agonum (Rhadine) koepkei* n. sp. C. *Agonum (Rhadine) tenebrosum* n. sp. D. *Agonum (Rhadine) exile* Barr and Lawrence.

Co., Texas, Oct. 19, 1957 (D. W. Tinkle and T. C. Barr). One paratype, "Amarillo, Texas" (U. S. N. M.), and one paratype (U. S. N. M.) from rodent burrow 11 mi. W. of Lamar, Bent Co., Colorado, Aug. 20, 1940 (G. M. Kohls and W. L. Jellison).

Diagnosis.—Similar to *A. longipes* Casey and *A. anthicoides* Casey, differing most conspicuously in the basal expansion of the pronotum, the dorsal tarsal grooves, and in having the 3rd antennal segment only 1/12, rather than 1/3 longer than the 4th.

Holotype.—TL 9.0, HL 1.96, HW 1.33, PL 1.97, PW 1.42, EL 5.10, EW 2.72.

Big Mouth Cave Sample of A. rubrum n. sp. (N = 5)

	R	M	S.D.	V(%)
TL	8.0-9.0	8.4	0.2	2.4
HW/HL	0.68-0.78	0.72	0.04	5.6
PW/PL	0.71-0.80	0.74	0.04	5.4
EW/EL	0.51-0.56	0.53	0.02	3.8
PL/HL	1.01-1.20	1.11	0.07	1.6
EL/PL	2.41-2.66	2.57	0.10	3.9

Description.—Length 8.0-9.0 mm. Form medium slender, depressed; pale, rufotestaceous. *Head:* 7/10 to 8/10 as wide as long; surface glabrous, shining, except for submental foveae, which are densely pubescent; frontal grooves broad and shallow; antennal ridge weak, extending only to anterior angle of eye (i.e., not continued as a supraorbital ridge); a rugulose area between frontal groove and antennal ridge; eyes moderately large and prominent, 1/5 of a head length. *Pronotum:* Elongate cordiform, 7/10 as wide as long, about 1/10 longer than head; apex 1/6 wider than base; maximum width before anterior marginal setae, which are placed at apical 1/6; pos-

terior setae in hind angles; surface glabrous, subconvex, the margins moderately reflexed, more so posteriorly; a short, lunate, postapical transverse sulcus; a much wider transverse sulcus separating off basal 1/6; sides broadly convergent and very gradually sinuate before the hind angles, which are small, subquadrate, slightly projecting; base shallowly emarginate between hind angles. *Elytra:* Medium full, half as wide as long, 2½ times as long as pronotum, strongly depressed and basolaterally deplanate; surface alutaceous, shining, glabrous; longitudinal striae feebly impressed but distinct; 2 to 4 discal punctures irregularly placed on the 3rd stria; marginal series of 16-18 setiferous punctures on 8th stria anteriorly, gradually moving onto 8th interval posteriorly; apices shallowly sinuate in basal 1/12 of elytra, acute, dehiscent, not produced. *Appendages:* Antenna reaching middle of elytra when laid back; segment II 5/12 or less as long as III; III about 1/12 longer than IV; dense pubescence beginning on apical half of IV, a lighter pubescence on III and apical half of II. First protarsomere dorsally grooved; proximal 3 meso- and metatarsomeres laterally grooved. Femora moderately robust, setae normal. Palps slender, elongate, finely pubescent, their last segments fusiform and finely but distinctly truncate. *Aedeagus:* 1.19 mm in paratype; arcuate, basal bulb but slightly enlarged, apex evenly attenuate; internal sac with minute, flat, rhomboid scales.

5. *Agonum (Rhadine) longicolle* (Benedict)
Fig. 2D

Rhadine longicollis Benedict 1928: 44. (Type: Snow Ent. Mus., Univ. of Kansas, Lawrence).

Agonum (*Rhadine*) *longicolle*, Csiki 1931: 849.

Length 9-11 mm, width 2.5-3.5 mm. Elongate slender, shining, rufopiceous, surface strongly alutaceous, generally glabrous. Head 6/10 as wide as long, widest at base of mandibles; sides strongly convergent behind eyes, which are 1/7 a head length; attached to prothorax by subglobular condyle; frontal grooves broad and shallow, extended over the eye; antennal ridge prolonged to posterior angle of eye; mentum tooth grooved medially but not actually bifid. Pronotum 7/10 to 8/10 as wide as long, about as wide as head, widest at the middle, sinuate in basal 1/5; a pair of marginal setae at apical 1/3, no basal setae; base emarginate, ¼ wider than apex; disc with numerous fine transverse impressions and a transverse groove at basal 1/5; anterior angles fine, acute; posterior angles larger, rounded, produced backward; margin finely reflexed; tip of prosternum acute as seen in full ventral view. Elytra elongate oval, 6/10 as wide as long, 2½ times as long as pronotum, strongly convex; margin finely reflexed, no apical sinus, apices separately rounded and scarcely produced or dehiscent; longitudinal striae shallow, faintly punctulate; 3 discal punctures on 3rd stria; 16-18 marginal punctures with comparatively short setae. An-

tennae half as long as body; segment IV 9/10 to 19/20 as long as III; moderate pubescence on apical half of III and on IV, denser on V-XI. Palps very faintly pubescent, the tips of the terminal segments finely but distinctly truncate, more so in labial palps. Mandibles porrect, moderate in length. Legs long and slender; mesofemora with about 5 long, stiff setae on undersides, metafemora with 2 or 3 setae, length of the setae equal to or a little less than a femoral width; tarsi with dorsal and lateral grooves. Aedeagus (Fig. 2D) 1.53-1.61 mm long, large, thick, the apex of the median lobe acute and strongly deflexed; vas deferens profusely clothed with long, slender, apiculate scales.

This species is known only from Carlsbad Caverns, Eddy Co., New Mexico, and nearby caves in Carlsbad Caverns National Park. Its diagnostic features are the wide head, sharply convergent behind the eyes; the grooved mentum tooth; one pair of pronotal marginal setae instead of the usual two; the acute prosternum; the rounded elytral apices; and the large aedeagus with deflexed apex and intensely scaly vas deferens.

6. *Agonum (Rhadine) howdeni* Barr and Lawrence
Fig. 2E

Barr and Lawrence 1960. Wasmann J. Biol., 18.

A troglophilic species frequenting the bat caves of Kerr, Edwards, and Uvalde Counties, south-central Texas, in the upper Nueces River basin. One specimen is known from southern Val Verde Co., Texas, from a cave near the mouth of the Pecos. *A. howdeni* is easily distinguished (from all but the next species) by the unusually long, stiff setae, more numerous and longer than in *longicolle,* on the under sides of the femora; by the absence of elytral longitudinal striation in the darker, fully sclerotized specimens; by the strongly convex, caudate elytra; and by the size and shape of the aedeagus (Fig. 2E).

7. **Agonum** *(Rhadine)* **babcocki** n. sp.
Fig. 2F

Type series.—Holotype male (U. S. Nat. Mus.), allotype female, and 40 paratypes, Mayfield's Cave, Sutton Co., Texas., Aug. 28, 1959 (Mills Tandy, B. C. Stewart, and T. C. Barr). Four paratypes, Mayfield's Cave, April, 1959 (M. Tandy, D. Widener). Sixteen paratypes (U. S. Nat. Mus.), Felton's Cave, Sutton Co., Texas, and 4 paratypes, Wheat Cave, Edwards Co., Texas (coll. by O. G. Babcock and F. C. Bishopp, 1926-1933). Four additional paratypes (U. S. Nat. Mus.), one from Wheat Cave (S. K. Jones, no date), and 3 from "Sutton Co., Texas" (R. H. Beamer, no date). One paratype, Iraan Cave, Pecos Co., Texas, September, 1958 (Royce Ballinger). Total type series 75 specimens.

Diagnosis.—A pale, slender, depressed species with caudate elytra and well-developed femoral setae, related to *howdeni* Barr and Lawrence but differing in the smaller eyes, the more slender body proportions, the consistently striate elytra, and the smaller and more slender aedeagus.

Holotype.—TL 9.61, HL 1.93, HW 1.15, PL 2.34, PW 1.29, EL 5.34, EW 2.71.

Mayfield Cave Sample of A. babcocki n. sp. (N = 20)

	R	M	S.D.	V(%)
TL	8.3-10.5	9.5	0.5	5.7
HW/HL	0.55-0.64	0.58	0.03	5.2
PW/PL	0.50-0.68	0.56	0.04	7.1
EW/EL	0.47-0.55	0.50	0.02	4.0
PL/HL	1.10-1.29	1.18	0.05	4.2
EL/PL	2.20-2.48	2.31	0.07	2.8
ANT 4/3	0.82-0.91	0.87	0.03	3.2

Description.—Length 8.3-10.5 mm. Elongate slender, depressed; pale rufotestaceous, shining. *Head:* 6/10 as wide as long, widest across the base of the mandibles; labrum 1/3 as long as wide, shallowly emarginate; frontal grooves short but deep; antennal ridge and lateral rugulae extending beyond posterior angles of eye; eye 1/6 of a head length, only slightly convex; surface shining, glabrous, microalutaceous. *Pronotum:* 5/10 to 7/10 as wide as long, averaging a little less than 6/10, widest just before the middle; apex 6/10 to 7/10 the maximum width, about 1/10 wider than base; margins evenly arcuate, subparallel the basal 1/10, moderately reflexed, more so behind the middle; anterior marginal setae at apical 1/3, posterior setae in hind angles; anterior angles small and rounded; posterior angles acute, small, blunt; base shallowly emarginate; disc shining, glabrous, microalutaceous, with faint transverse striae near the middle. *Elytra:* Elongate oval, subconvex, half as wide as long, about 2¼ times as long as pronotum; disc scattered with very fine pubescence, shining; microsculpture isodiametric, feebly transverse; margin moderately reflexed to the sinus in apical 1/9; apices produced, acute, dehiscent; longitudinal striae very shallow but distinct; some individuals with 2 small discal punctures on 3rd interval; marginal setiferous punctures 14-16. *Appendages:* All long and slender. Mandibles rather long; terminal palpal segments weakly truncate, fusiform, with very fine pubescence. Antenna when laid back extending to middle of elytra; segment IV 8/10 to 9/10 as long as III; dense pubescence beginning on apical 2/3 of IV. Legs more slender than in *A. howdeni,* but with similar development of long setae on the under sides of the meso- and metafemora; setae in two rows of 4-6 each, about equal in length to a femoral width. *Aedeagus:* (1.40-1.46 mm) a little smaller and more slender than in *howdeni;* basal bulb slightly enlarged, bearing a small keel; distal portion of vas deferens armed ventrally with scales (as in *howdeni*), proximal portion with long, slender scales.

Remarks.—*A. babcocki,* compared with *howdeni,* is smaller and more slender, as reflected in the values TL, HW/HL, PW/PL, and EW/EL. The margin of the pronotum in *howdeni* shows a slight subapical sinuation not present in *babcocki,* and the base is a little more constricted. In *howdeni* the pronotal apex is about 1/6 wider than the base, and in *babcocki* the apex is 1/9 to 1/10 or less wider than the base.

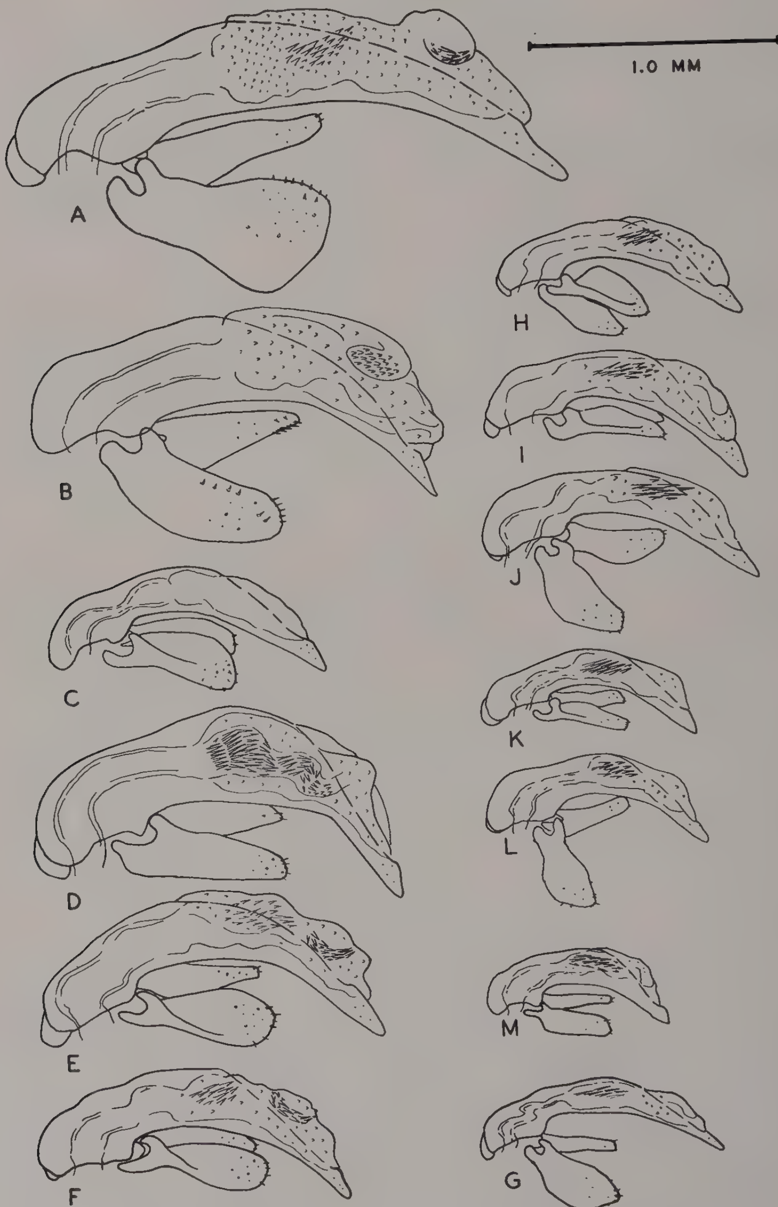

Fig. 2.—Aedeagi of *Agonum (Rhadine)* spp. Camera lucida sketches. A. *caudatum* (Lec.), Warren Co., Tenn. B. *jonesi* n. sp., paratype. C. *rubrum,* n. sp., paratype. D. *longicolle* (Benedict), topotype. E. *howdeni* Barr and Lawrence, paratype. F. *babcocki* n. sp., paratype. G. *subterraneum* (Van Dyke), Williamson Co., Texas. H. *infernale* s. str. Barr and Lawrence, paratype. I. *infernale ewersi* n. subsp., paratype. J. *koepkei* n. sp., paratype. K. *tenebrosum* n. sp., paratype. L. *specum* n. sp., holotype. M. *exile* Barr and Lawrence, paratype. (The variable appearance of the parameres is partly the result of different orientation.)

8. *Spelaeorhadine araizai* Bolívar

Spelaeorhadine araizai Bolívar 1944:28.

This species, known only from La Gruta Palmito, near Bustamante, Nuevo Leon, Mexico, seems very close to *A. howdeni* and *A. babcocki,* to which it is possibly allied by the unusual development of the femoral setae. The presence of these long setae in the two central Texas species, as well as in *longicolle* (Benedict) and *longiceps* (Van Dyke), and the variable development of the femoral setae in other species of *Rhadine* indicate the unreliability of this character for generic diagnoses. Bolívar's description is that of a bona fide *Rhadine,* and *Spelaeorhadine* should probably be regarded as a junior synonym of *Agonum* sens. lat. Unfortunately I have been unable to obtain a specimen of *S. araizai* for examination and comparison with the Texas species.

9a. *Agonum (Rhadine) infernale infernale* Barr and Lawrence

Agonum (*Rhadine*) *infernale* Barr and Lawrence 1960. Wasmann J. Biol., 18.

Length 6.6-8.2 mm. Head half as wide as long, abruptly constricted behind and expanded into a subglobular condyle; surface shining, isodiametrically microgranulate, with a sparse scattering of pubescence; eye pale without facets, about 1/20 of a head length in diameter. Pronotum 6/10 as wide as long, widest at the middle, slightly sinuate before the base; base 5/7 the maximum width, slightly narrower than apex; angles small and rounded. Elytra 6/10 as wide as long, widest just beyond the middle, with a very shallow sinus in apical 1/7; apices somewhat acute and dehiscent, not greatly produced; surface convex, dull shining, microalutaceous, longitudinal striae obsolete; marginal punctures about 14, with long, whip-like setae in 3rd, 9th, and 12th punctures. Last segments of maxillary and labial palps finely truncate (Fig. 3A). Segment IV of antenna 1/10 to 1/20 shorter than III. Aedeagus (Fig. 2H) 1.01-1.13 mm long, slender, elongate, arcuate, apex attenuate; vas deferens with long, slender scales.

Known from Madla and Marnock Caves, near Helotes, in the highlands north of San Antonio, Bexar Co., Texas, and from Alzifar Cave (determination based on a single female), on the Koepke Ranch, 11 miles NE. of Boerne, Kendall Co., Texas.

9b. **Agonum** *(Rhadine)* **infernale ewersi** n. subsp.

Figs. 1A, 2I

Type series.—Holotype male (Cincinnati Museum of Natural History), allotype female, and 12 paratypes, Headquarters Cave, Camp Bullis, Bexar Co., Texas, April 19 and May 10, 1959 (Ralph Ewers).

Holotype.—TL 7.7, HL 1.84, HW 0.97, PL 1.66, PW 1.10, EL 4.28, EW 2.39.

Headquarters Cave Sample of A. infernale ewersi n. subsp. (N = 12)

	R	M	S.D.	V(%)
TL	7.6-8.8	8.0	0.4	4.4
HW/HL	0.50-0.57	0.54	0.02	4.3
PW/PL	0.62-0.73	0.68	0.03	5.0
EW/EL	0.52-0.57	0.55	0.02	2.7
PL/HL	0.83-0.95	0.89	0.03	3.7
EL/PL	2.42-2.68	2.55	0.08	3.1
ANT 4/3	0.86-0.95	0.92	0.03	3.6

Description.—Similar to *infernale* s. str. in general appearance—eyes 1/20 of a head length; terminal palpal segments pubescent, truncate; elytra dull shining, longitudinal striae obsolete.

Analysis of the statistics for the Madla Cave population of *infernale* s. str. (Barr and Lawrence 1960) and the Headquarters Cave population of *ewersi* n. subsp. reveals the following significant variations for the latter ($P < 0.01$ by t test): (1) greater total length, (2) wider pronotum (about 7/10 as wide as long instead of 6/10, (3) elytra longer and more slender, and (4) segment IV of antenna slightly longer with respect to III. The aedeagus does not differ appreciably from that of *infernale* s. str.; four aedeagi of *ewersi* ranged between 1.12 and 1.15 mm, mean length 1.14 mm.

10. **Agonum** *(Rhadine)* **koepkei** n. sp.

Figs. 1B, 2J, 3C

Type series.—Holotype male (Cal. Ac. Sci., ent.), allotype female, and 70 paratypes, Schneider's Ranch Cave, 14 mi. NE of Boerne, Kendall Co., Texas, Aug. 29, 1959 (H. M. Koepke and T. C. Barr). Nine paratypes (Cincinnati Mus. Nat. Hist.) from a small, unnamed cave near Sisterdale, north of the Guadalupe, Kendall Co., Texas, April 15, 1959 (Ralph Ewers).

Diagnosis.—A microphthalmous *Rhadine* with obsolete elytral striation, closely related to *A. infernale* but differing in the rounded tips of the terminal palpal segments, the subequal III and IV antennal segments, and the proportionately longer head.

Holotype.—TL 7.6, HL 1.79, HW 0.92, PL 1.80, PW 1.06, EL 4.05, EW 2.30.

Schneider's Ranch Cave Sample of A. koepkei n. sp. (N = 20)

	R	M	S.D.	V(%)
TL	7.0-7.9	7.5	0.3	2.8
HW/HL	0.47-0.54	0.51	0.02	3.9
PW/PL	0.53-0.61	0.57	0.02	3.5
EW/EL	0.52-0.59	0.56	0.02	3.6
PL/HL	0.95-1.13	1.01	0.05	5.0
EL/PL	2.19-2.41	2.30	0.19	8.3
ANT 4/3	0.97-1.09	1.01	0.02	2.0

Description.—Length 7.0-7.9. Elongate slender; head and pronotum shining, elytra dull shining; dark rufotestaceous; sparsely pubes-

cent. Eyes pale without facets, about 1/20 a head length; base of head constricted and then expanded into a subglobular condyle, which is less pronounced than in most of the microphthalmous species. *Pronotum*: About as in *infernale* s. str., averaging a little less than 6/10 as wide as long, about equal to head in length. *Elytra*: Averaging 11/20 as wide as long, longitudinal striae obsolete except in pale, recently emerged specimens; surface alutaceous, dull shining; apex as in *infernale*. Labial and maxillary palps pubescent, the last segments fusiform, not swollen; the apices rounded, neither truncate nor produced, glabrous, pale or hyaline. Segments III and IV of antenna subequal in length; moderate pubescence beginning on III, a little denser on IV-XI. *Aedeagus:* Not differing appreciably from that of *infernale*, measuring 1.15-1.19 mm in length.

11. **Agonum** *(Rhadine)* **tenebrosum** n. sp.
Figs. 1C, 2K, 3B

Type series.—Holotype male (Canadian Nat. Coll. No. 7118), allotype female, and 12 paratypes, Wilson's Cave, 25 mi. SW of Hunt, Kerr Co., Texas, Mar. 31 and April 9, 1959 (Becker, Howden, and McAlpine). Six paratypes, cave on Humble Oil Pumping Station "C" property, near Hunt, Kerr Co., Texas, Mar. 21, 1959 (Ralph Ewers).

Diagnosis.—Similar to *infernale* in having the tips of the last palpal segments truncate, differing most conspicuously in the retention of longitudinal elytral striae, the advanced degree of pubescence, the smaller aedeagus, and the more slender body proportions.

Holotype.—TL 7.1, HL 1.75, HW 0.87, PL 1.66, PW 0.88, EL 3.68, EW 1.93.

Wilson's Cave Sample of A. tenebrosum n. sp. (N = 14)

	R	M	S.D.	V(%)
TL	6.3-8.0	7.2	0.5	6.6
HW/HL	0.44-0.51	0.47	0.02	4.3
PW/PL	0.49-0.56	0.52	0.02	4.3
EW/EL	0.50-0.54	0.52	0.01	2.2
PL/HL	0.88-1.00	0.95	0.03	3.2
EL/PL	2.05-2.38	2.23	0.09	4.1
ANT 4/3	0.79-1.00	0.89	0.05	5.5

Description.—Length 6.3-8.0 mm. Elongate, slender; shining rufotestaceous, pubescent. *Head:* Half as wide as long, widest at base of mandibles and attached to prothorax by a subglobular condyle; genae, gula, and submentum with scattered, rather long pubescence and frons and vertex with shorter pubescence; labrum bisinuate; frontal grooves short, antennal ridge and rugulae attaining posterior angle of eye and beyond; eye about 1/20 a head length. *Pronotum:* Half as wide as long; widest in basal 3/7; apex and base subequal, 2/3 the maximum width; anterior marginal setae at apical 2/7, posterior setae in hind angles; disc lightly pubescent, subgranulate, a few medial transverse striae; margin with evident sinuation before anterior setae and again before the hind angles, which are small, acute, rounded. *Elytra*:

Elongate, convex, apical sinus shallow, apices acute, finely dehiscent; interstriae with well-developed rows of fine pubescence; longitudinal striae feeble but distinct, faintly punctulate; two weak discal punctures on 3rd interval; usual number of marginal punctures 14, with whip-like setae in 3, 9, and 13. *Appendages:* Palps pubescent, the apices of the terminal segments rounded, pale, glabrous. Antenna with all segments decidedly pubescent except I, denser pubescence beginning on IV; segment III a little longer than IV. *Aedeagus:* 0.91-0.93 mm long, short, weakly arcuate, slender, apex rather attenuate.

12. **Agonum** *(Rhadine)* **specum** n. sp.
Figs. 2L, 3E

Type series.—Holotype male (Cal. Acad. Sci. ent.), and allotype female. Cave-Without-A-Name, Kendall Co., Texas, August 25, 1959 (T. C. Barr); female paratype, Cascade Caverns, Kendall Co., Texas, August, 1959 (H. M. Koepke); female paratype (Cincinnati Mus. Nat. Hist.), Alzifar Cave, on the Koepke Ranch, Kendall Co., Texas, March 15, 1959 (R. Ewers).

Diagnosis.—A slender microphthalmous species with the last segments of the palps swollen and apically produced as in *exile* Barr and Lawr., differing from *exile* in not having the head sharply constricted behind; in the higher head, pronotal, and elytral indices and the higher EL/PL (ranges of all ratios mutually exclusive); and in the larger aedeagus; differs from *subterraneum* (Van Dyke) in the larger eyes, the presence of 2 pairs of pronotal setae, and the smaller and more arcuate aedeagus.

Holotype.—TL 6.81, HL 1.56, HW 0.74, PL 1.75, PW 0.77, EL 3.50, EW 1.61, aedeagus 0.91.

Type Series of A. specum n. sp. (N = 4)

	R	M
TL	6.5-8.3	7.4
HW/HL	0.43-0.47	0.45
PW/PL	0.40-0.45	0.43
EW/EL	0.47-0.48	0.48
PL/HL	1.06-1.12	1.08
EL/PL	2.00-2.12	2.05
ANT 4/3	0.88-0.97	0.91

Description.—Length 6.5-8.3 mm, maximum width (elytra) 1.6-2.1 mm. Elongate, very slender; shining, pale rufotestaceous; similar to *exile* when not otherwise specified below. *Head:* Less than half as wide as long; surface with scattered, rather coarse pubescence, shining; not sharply constricted posteriorly, i.e., condyle for articulation with prothorax not subglobular. *Pronotum:* 4/10 as wide as long, widest just behind the middle; base slightly wider than apex, 7/10 the maximum width; anterior marginal seta just behind apical ¼, posterior seta in hind angle; surface glabrous, shining, indistinctly granulate; margin subparallel in apical 1/7 and basal 1/20, gently arcuate between. *Elytra:* Subconvex, not quite half as wide as long and fully twice as long as pronotum; surface shining, sparsely pubescent; longitudinal striae shallow but distinct; marginal punctures 14; some spe-

cimens with a small puncture on 3rd interval behind the middle. *Appendages:* Palps pubescent, their last segments fusiform, slightly swollen, the apex produced, pale, and glabrous. Antenna when laid back reaching beyond middle of elytra. *Aedeagus:* 0.91 mm long in holotype.

13. *Agonum (Rhadine) exile* Barr and Lawrence
Figs. 1D, 2M, 3F

Agonum (Rhadine) exile Barr and Lawrence 1960. Wasmann J. Biol., 18.

This extremely slender, depressed species (7.0-8.4 mm long by 1.4-1.8 mm wide) is known only from caves near Helotes and Camp Bullis in the upland north of San Antonio, in northern Bexar Co., Texas. It may be distinguished by the low width/length indices for the head, pronotum, and elytra (Barr and Lawrence 1960); the swollen terminal palpal segments, finely and densely pubescent with abruptly attenuate, produced tips; consistently striate elytra; and the unusually small aedeagus (0.71-0.77 mm).

14. *Agonum (Rhadine) subterraneum* (Van Dyke)
Figs. 2G, 3D

Comstockia subterranea Van Dyke 1918:172. (Type: Sam Bass Cave, McNeil, Travis Co., Texas; Cornell Univ., Dept. Ent. Coll.).

Agonum (Rhadine) subterraneum, Barr and Lawrence 1960. Wasmann J. Biol., 18.

Diagnosis.—A microphthalmous cave species with the last palpal segments swollen, pubescent, apically produced, and with the greatest width of the pronotum in its basal third; easily distinguished by the microscopic eyes (about 0.025 mm) and the absence of the posterior pair of pronotal setae.

Type female.—TL 7.9, HL 1.75, HW 0.74, PL 1.93, PW 0.78, EL 4.18, EW 1.98, ANT 4/3 0.94.

Beck's Ranch Cave Sample of A. subterraneum (Van Dyke) (N = 13)

	R	M	S.D.	V(%)
TL	7.3-8.9	7.9	0.5	6.3
HW/HL	0.40-0.45	0.42	0.02	4.8
PW/PL	0.39-0.46	0.42	0.02	4.8
EW/EL	0.43-0.58	0.49	0.03	7.0
PL/HL	1.00-1.17	1.09	0.05	4.6
EL/PL	1.93-2.22	2.05	0.08	4.1
ANT 4/3	0.90-1.00	0.94	0.02	2.6

Description.—Length 7.3-8.9 mm. Form very slender and elongate; head and thorax shining, elytra dull shining; rufotestaceous. *Head:* Extremely narrow, elongate behind the bases of the antennae, constricted at neck, attached to prothorax by a subglobular condyle; surface glabrous except for pubescent submental foveae; labrum feebly bisinuate; frontal grooves shallow, broad; antennal ridge weak; eyes almost completely absent, their site indicated by a tiny, pale spot the diameter of a supraorbital puncture (about 0.020 x 0.025 mm). *Pro-*

notum: Greatly elongate, 4/10 as wide as long, widest in basal 1/3, 1/5 wider than head; apex ¾ as wide as base and half the maximum width; surface glabrous, with a median subconvex ridge and lateral flattened areas near the margin, which is narrow and slightly reflexed; anterior angles effaced; posterior angles small, acute, rounded; both pairs of marginal setae absent. *Elytra:* Elongate elliptical, a little less than half as wide as long and twice as long as the pronotum; surface glabrous, alutaceous; apical sinus shallow, apices acute, dehiscent, only slightly produced; longitudinal striae feeble but distinct; a pair of small discal setae on the 3rd stria behind the middle; marginal punctures usually 12, with long, whip-like setae in the 3rd, 9th, and 11th punctures. *Appendages:* Mandibles of moderate proportions; maxillary and labial palps densely pubescent, the terminal segments fusiform, somewhat enlarged, their apices produced, pale white, glabrous. Antennae long and slender, attaining the apical third of the elytra when laid back; segment III slightly longer than IV; dense pubescence beginning on IV, sparse pubescence on III and apical half of II. Legs long and quite slender; no grooves on front tarsi. *Aedeagus:* 1.10-1.17, mean of 4 specimens 1.12 mm; basal bulb expanded; median lobe very slender, weakly arcuate in the mid-portion, apically attenuate; vas deferens with proximal patch of long, slender, apiculate scales.

EVOLUTION OF CAVERNICOLE RHADINE

That members of the subgenus *Rhadine* are preadapted for a cave existence is readily seen from the common occurrence of its normally epigean species (a) either in caves, cellars, or mammal burrows, or (b) in cool, moist environments beneath decaying logs, at high elevations.

The cavernicolous *Rhadine* may be arbitrarily divided into three groups: (1) facultative troglophiles — normally epigean species which are not uncommon in caves but show no special modifications associated with cave life — including *caudatum, jonesi* (?), *ozarkense* (?), and *rubrum;* (2) habitual troglophiles — species known only from caves but with comparatively large eyes — including *longicolle, howdeni, babcocki,* and probably *Spelaeorhadine araizai;* and (3) troglobites, including *infernale, koepkei, tenebrosum, specum, exile,* and *subterraneum.*

The facultative troglophiles include at least two species groups: *caudatum, jonesi,* and *ozarkense* are obviously closely related, and *rubrum* is allied to *anthicoides* Csy. and *longipes* Csy. Careful collecting in western caves will probably reveal other normal epigean species which can readily colonize suitable caves. At the present time *jonesi* and *ozarkense* are known only from the type caves, yet their lack of special cave modifications indicates that this is perhaps a result of inadequate and unsystematic collecting.

Among the habitual troglophiles *howdeni* and *babcocki* are so similar that they could perhaps be regarded as sibling species. *A. longicolle* approaches *howdeni* and *babcocki* in its slender form and in

the hypertrophy of the femoral setae, but its rounded elytral apices and the larger, thicker aedeagus with intensely scaly vas deferens bespeak other affinities and suggest convergence. *S. araizai* is probably allied to *howdeni* and *babcocki*.

The six known species of troglobites are characterized by reduction in size, slender body and appendages, development of pubescence, reduction in eyes, and by hypertrophy of the elytral marginal setae, three of which are typically long and whip-like. Three of the species — *exile, specum,* and *subterraneum* —exhibit an unusual modification of the last segment of the labial and maxillary palps, which has become fusiform, swollen, and produced at the apex. *A. infernale* and *A. tenebrosum,* with their truncate palpal segments, are probably the most primitive forms and share a close common ancestry with *koepkei,* which is intermediate in palpal development, the last segment being fusiform and apically rounded but not swollen or produced. The slender body form reaches its highest development in *exile* and *subterraneum,* and the extreme palpal enlargement and attenuation is found in *exile* and *specum.* Pubescence may be sparse, as in *infernale,* or extreme, as in *tenebrosum,* the other four species occupying intermediate positions with respect to this character. The trend toward eye reduction culminates in *subterraneum,* though the eye is distinctly smaller in *exile* than in *infernale, tenebrosum, koepkei,* and *specum.* All six species probably represent a single phyletic line. There are no known epigean representatives of this species group.

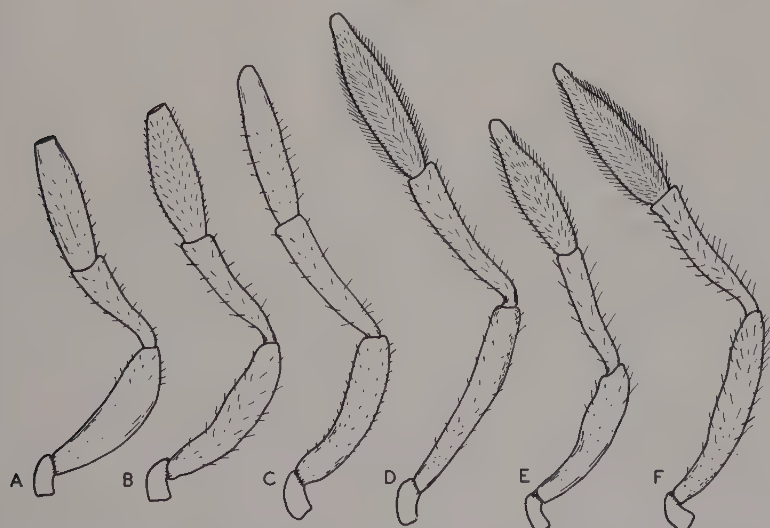

Fig. 3.—Right maxillary palp of *Agonum (Rhadine)* spp., ventral view. A. *infernale* s. str. Barr and Lawrence. B. *tenebrosum* n. sp. C. *koepkei* n. sp. D. *subterraneum* (Van Dyke). E. *specum* n. sp. F. *exile* Barr and Lawrence.

At least seven evolutionary trends may be noted among the habitual troglophiles and the troglobites: (1) reduction in size, (2) reduction in eyes, (3) slender body and appendages, (4) development of pubescence, (5) rounding of the apex of the last palpal segments, with a tendency toward enlargement and attenuation, (6) hypertrophy of the femoral setae, and (7) hypertrophy of elytral marginal setae. The last three are in all probability tactile modifications of positive adaptive value in an aphotic environment. Reduction in size and acquisition of a slender body and slender, elongate appendages are commonly regarded as adaptations to moving about through narrow crevices, though there are possibly as yet unrecognized selective factors favoring these modifications. No wholly satisfactory explanation for the increase in pubescence — common among cave carabids of the tribe Trechini — is known to me at the present time. I prefer to regard the reduction of eyes as the result of mutation pressure unopposed by selection pressure (a theory of regressive evolution first espoused, I think, by August Weismann). Whether the greater eye reduction in *subterraneum* reflects a correspondingly longer evolutionary history underground, a more rapid rate of regression, or early fortuitous fixation of a complex of recessive alleles, I do not know.

Speciation in Cavernicole Rhadine

One might suppose that the absence of wings, a high humidity requirement, and the burrowing habit would serve rapidly to isolate various populations of *Rhadine*, giving rise to numerous local species. This may be true in the warm, arid or semi-arid regions of the southwest, but as a general rule this concept is seriously questioned by the widespread distribution of *A. caudatum*, known from Maryland west to central Illinois and south to Virginia, Tennessee, and Alabama. Possibly future collecting will show *A. jonesi* to be a coastal plain species, replacing *caudatum* below the fall line. *A. ozarkense* may possibly fill the *caudatum* niche in the Ozark Plateau.

The closest known relative of *A. longicolle* is unquestionably *A. longiceps* (Van Dyke), from the vicinity of Alpine, Texas, a species with which it shares the grooved mentum tooth, single marginal pronotal seta, non-caudate elytra, and intensely scaly vas deferens. The two forms are allopatric and their differences are minor ones, yet the smaller aedeagus in *longiceps,* without the sharply deflexed apex characteristic of *longicolle,* suggests (as in the case of *caudatum* and *jonesi*) that the corresponding gene pools have drifted far enough apart that there is no exchange between them.

A similar situation exists between *A. howdeni* and *A. babcocki,* two allopatric species closely resembling each other. Their known geographic ranges are mutually exclusive yet nearly contiguous. Aedeagal differentiation admits only the interpretation of genetic discontinuity, yet these two species cannot be far from the point of divergence.

The two stocks of the troglobite species present the same picture of recent divergence on a geographically smaller scale. The interpretation of the *known* distribution of the *known* six species is fraught with alternative hypotheses, some of which are, however, susceptible to future testing by careful collecting in specified areas.[1] The suggested phylogeny of the known species is diagrammed in Figure 4, with the five points of genetic divergence indicated by s_1-s_5 and the two principal stocks by A_1 and A_2, stock A_0 representing the presumed epigean ancestor of the species group. For the purposes of the following discussion it is assumed that speciation in each case has been allopatric.

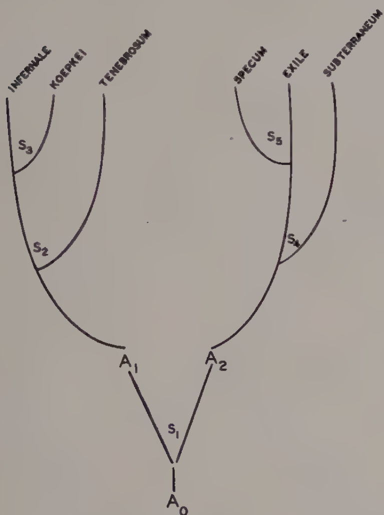

Fig. 4.—Phylogeny of Texas troglobite *Agonum (Rhadine)* of the *subterraneum* group. Explanation in text.

The late Pliocene or early Pleistocene stream levels at the eastern edge of the Edwards plateau are represented by deposits known as the Uvalde gravels, which occur in terraces high above the present streams. These streams entered upon their present erosional cycles with the inferred uplift of the plateau at the onset of the Pleistocene. Probably none of the caves at the eastern margin of the plateau is any older than early Pleistocene. Stock A_1 has diverged at least twice (s_2 and s_3) since its original colonization of the caves of the Guadalupe River basin. *A. tenebrosum* is regarded as a derivative of A_1 by headward dispersal through subterranean channels associated with development of the Guadalupe (see Barr, 1959, for discussion of this means of dispersal in cavernicole carabids). These channels are more likely to be continuous near the headwaters of the stream, and *tenebrosum* now seems to be wholly disjunct from both downstream species descended

[1] It is recognized that additional collecting to substantiate a hypothesis frequently (at least among cavernicoles) invalidates one or more of the assumptions by which the original question was formulated!

from A_1. *A. infernale* and *A. koepkei* are morphologically and geographically much closer to each other than to *tenebrosum*, and are separated only by the Guadalupe River, which, by deepening and widening its channel, apparently effected complete disjunction (s_3) of the populations of A_1 along its left and right banks. The divergence s_2 was probably earlier than s_3, on both morphological and geological grounds. A thorough biological exploration of Guadalupe valley caves, especially between Sisterdale and Hunt, would be most interesting if it yielded additional specimens of troglobite *Rhadine*. A gap of at least 50 miles, as the river flows, remains in our knowledge of the distribution of stock A_1. It is possible that undiscovered disjunct populations exist in isolated relicts of the Guadalupe cave network.

If *specum-exile* and *subterraneum* are in fact close relatives (as I believe), and not the product of convergent evolution, one is confronted with two alternatives: (1) the ancestral stock A_2 successfully and independently colonized caves in both the San Antonio and Austin areas, or (2) stock A_2 successfully colonized caves only once, and by a process of dispersal along underground stream channels and consecutive transfer by subterranean stream piracy has extended its range 80 miles or more along the Balcones fault zone from the Colorado River drainage system to the Guadalupe. If the latter hypothesis is correct, we could expect the discovery of related species in the intervening caves of Travis, Hays, Comal, and Blanco Counties.

The disjunction (s_5) between *specum* and *exile* cannot be satisfactorily explained at present. *A. specum* is found in the caves excavated in the limestones at the top of the Trinity group (Glen Rose) at lower elevations than the upland caves at Helotes and Camp Bullis, which are developed in limestone of the Fredericksburg group capping an outlier of the plateau. It is possible, on geologic grounds, that the upland and lowland cave systems are distinct and mutually exclusive, but the single female *A. i. infernale* from Alzifar Cave, just south of the Guadalupe, argues against this view, since it indicates that *infernale* ranges across the supposed barrier. Clearly more specimens of both species are required from the lowland caves around Boerne.

SUMMARY

Descriptions and a key to species are given for the 13 known cavernicole species of the subgenus *Rhadine* (genus *Agonum*) from the United States: *caudatum* (Lec.), *jonesi* n. sp., *ozarkense* (Sanderson and Miller), *rubrum* n. sp., *longicolle* (Benedict), *howdeni* Barr and Lawrence, *babcocki* n. sp., *infernale infernale* Barr and Lawrence, *infernale ewersi* n. subsp., *koepkei* n. sp., *tenebrosum* n. sp., *specum* n.sp., *exile* Barr and Lawrence, and *subterraneum* (Van Dyke). Evolutionary trends and speciation in the group are discussed, with particular reference to the microphthalmous, troglobite species from the Edwards plateau of Texas.

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Cavernicolous Pselaphid Beetles of the United States[1]

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CONTENTS

Introduction

Cavernicolous Pselaphidae have been known from Europe for over a century, *e.g., Machaerites spelaeus* Miller, 1855 and *M. subterraneus* (Motschulsky), 1859, both from caves in Carniola, that is to say, northeastern Italy-northwestern Yugoslavia (Jeannel, 1950).

By contrast, American cavernicolous pselaphids were unknown prior to 1951 and since this date have received considerable attention (Park, 1951, 1956, 1958). About the same time cavernicolous pselaphids of Japan were reported by Yoshida and Nomura (1952), and more recently by Jeannel (1958).

The present study reviews the status of North American cavernicolous pselaphids, describes thirteen new taxa, and discusses the zoögeographic and evolutionary patterns exemplified by the group. A key to tribes, genera and species is included.

At the present time there are three tribes, six genera, and thirty-three species known to inhabit caves in North America, chiefly limestone caverns in the southern Appalachian system of mountain ranges and plateaus. Collection of this material has occupied the effort and time of many people. Primarily in the order of reception of research material, these gentlemen are as follows: Walter B. Jones, State Geologist of Alabama; J. Manson Valentine, Highlands, North Carolina; René Jeannel, Muséum National d'Histoire Naturelle, Paris; Thomas C. Barr, Jr., Tennessee Polytechnic Institute; Leslie Hubricht, Louisville, Kentucky; Carl H. Krekeler, Valparaiso University; Harrison R. Steeves, Birmingham, Alabama; Walter R. Suter and John A. Wagner, Northwestern University. The author thanks them for their help, without which this report would have been impossible.

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[1] Some of the data in this report were presented on December 28, 1959, at a symposium sponsored by the National Speleological Society and the Society of Systematic Zoology at the Chicago meetings of the American Association for the Advancement of Science.

SYNONYMIES AND DESCRIPTION OF NEW TAXA

Recent investigations since my last report (Park, 1958) have revealed the presence of thirteen new populations, herein described, and have indicated the need to synonymize various taxa.

Arianops *(Arispeleops)* stygica new species

Type Male. Head 0.53 mm long x 0.42 mm wide; pronotum 0.53 x 0.47; elytra 0.67 x 0.67; abdomen 0.8 x 0.67; total length 2.53 mm.

Moderate shining brown with subimpunctate integuments; pubescence rather sparse, long and appressed except bristling on genal areas.

Head with eyes absent; the conventional replacing spine absent and in turn replaced by an inconspicuous tumulus at end of the clypeo-genal carina; tempora long and convergent; vertex with a pair of small vertexal foveae near occiput; occiput scabro-striate medianly and weakly bisected by a low carina to a point between vertexal foveae; a rather conspicuous, subquadrate concavity between the widely separated antennal tubercles; front simple, declivous and bounded by a strong clypeal-genal flange; labrum transverse with acute angles and bearing a pair of cusps at center of distal margin; left mandible crossed dorsal to right; ventral surface of head and maxillary palpi as for *cavernensis*.

Antennae 1.4 mm long, slender, widely separated, eleven-segmented; first nine segments longer than wide, I and II relatively large, III to VIII subequal in width, eighth shorter; club of last three segments, IX elongate oval with ventral face slightly concave apically, much larger than eighth; X with width equal to length, as long as eighth, suboval; XI largest segment, as long as preceding three segments united, with apical end rather abruptly tapered and heavily pubescent.

Pronotum as wide as head, longer than wide, rounded truncate-oboval, disc simple and convex; six baso-lateral foveae placed as follows, one on each side of center of base, one on each side at lateral third of length, and one each side between these two; basal margin transversely microstriate-alutaceous.

Elytra with long, gently sloped humeri; base of each elytron raised in a carinoid margin; elytron with neither antebasal nor subhumeral foveae, lacking any discal impression, but with an entire and well developed sutural stria, flank with a carina which arises at basal third of lateral margin and continues obliquely to distal margin.

Abdomen with five tergites in median length ratio of 4.5/1.6/1.2/9.5/2.0. First tergite with a pair of short basal abdominal carinae obscured by pubescence. Fifth tergite with a very conspicuous fovea at center of upper margin of posterior face. Seven sternites in median length ratio of 1.0/4.0/1.3/1.0/-1.0/2.0/1.5. Third sternite bearing at center a short cusp; seventh sternite in the form of a triangular aedeageal plate. This plate is entirely surrounded by the deeply incised fifth tergite and the concave sixth sternite, this latter bears a foveoid concavity on each side of generally concave surface.

Prosternum, mesosternum and mesocoxal cavities as described for *jeanneli*, but the metasternum bears a very prominent fovea near posterior margin. Legs long, slender, unarmed, with last tarsomere bearing a rather short claw and a shorter divergent accessory claw.

Described on one male, the type, in author's collection. Collected by Leslie Hubricht and T. C. Barr, Jr. in Cumberland Caverns, Warren County, Tennessee on June 23, 1957.

This new species is not too closely related to other members of the genus. By the absence of the median antebasal fovea and cusps it belongs in the subgenus *Arispeleops;* six baso-lateral foveae are similar to *Arianops* (*Arianops*) *amplyoponica* (Brendel), 1890 and *plectrops* Casey, 1897.

Batrisodes *(Babnormodes)* **gemmoides** new species

Type Male. Head 0.44 mm long x 0.45 mm wide; pronotum 0.44 x 0.44; elytra 0.64 x 0.60; abdomen 0.50 x 0.67; total length 2.0 mm.

Shining reddish brown, with moderately long and sparse pubescence which is bristling in genal areas, semierect on pronotum and elytra, and almost prostrate on abdomen. Integuments polished and weakly asperate-micropunctulate.

Head with moderately prominent eyes of about 40 facets; lateral vertexal carinae well developed; vertex convex between the two nude, deep vertexal foveae; U-shaped interfoveal sulcus which becomes evanescent apically; face (front and clypeus) dorsally gently declivous between antennal tubercles, this area with microsetae, each seta in a minute asperity and the frontal margin blackened and medianly extended to give a rounded-triangular outline; this frontal margin slightly overhanging the lower face; lower face more steeply declivous and bears medianly an inconspicuous longitudinal tubercle; lower clypeal area sparsely microgranulate.

Antennae with segment X slightly flattened on ventral face; segment XI with ventral face flattened and bearing a small poroid scar.

Pronotum, elytra, abdomen and legs essentially as for subgenus *Babnormodes* and very similar to *subterraneus* as described previously (Park, 1951:30). Abdomen with five visible tergites in median length ratio of 4.5/2.0/1.5/2.5/1.8 with first tergite bearing a pair of basal abdominal carinae that are about one-fifth as long as segment and separated by about 23 percent of total tergite width; fifth tergite with posterior margin slightly concave medianly, this tergite vertical. Five sternites fully visible, in median length ratio of 2.2/1.0/0.8/1.0/2.0 with the posterior margin of the fifth sternite slightly convex medianly.

Female similar to male except that (1) the eyes are smaller, of about 10 facets; (2) face rather uniformly and steeply declivous between antennal tubercles, without a frontal margin, lacking a median tubercle and the declivity very sparsely microgranulate; (3) antennal segments X and XI simple, with convex unmodified ventral faces; (4) mesotarsi not abnormally formed.

Described on a pair, type and paratype in author's collection, collected by T. C. Barr, Jr., in Columbia Caverns, Dickson County, Tennessee on March 5, 1957.

Within the subgenus *Babnormodes, gemmoides* has the entire, blackened, produced, frontal margin of *gemmus* (Park, 1956:71) and both species have a clypeal tubercle. On the other hand, *gemmoides* has the distal (eleventh) antennomere with ventral face flattened and bearing a small poroid scar near mesio-basal angle, whereas this segment in *gemmus* is simply convex and unmodified. The description of the eleventh antennal segment in *gemmoides* is the same as in *barri* (Park, 1958:40), but *barri* has the ventral face of the tenth antennal

segment bearing a conspicuous fovea. These three species appear to form a species group within the subgenus, and all three are from caves in Dickson County, Tennessee. *Gemmus* is known from Jewel Cave; *gemmoides* from Columbia Caverns; and *barri*, described from Dickson Cave, has also been collected from Columbia Caverns. This latter collection (T. C. Barr, Jr., June 22, 1957) of *barri* in the type locality of *gemmoides* placed two allied species in the same cave. The two species are very distinct from each other in numerous cephalic and antennal details and are not difficult to separate taxonomically.

Batrisodes *(Babnormodes)* **ferulifer** new species

Type Male. Head 0.47 mm long x 0.47 mm wide; pronotum 0.47 x 0.46; elytra 0.7 x 0.8; abdomen 0.74 x 0.67; total length 2.4 mm.

Moderately shining dark reddish brown; pubescence long, sparse but flavous and obvious against the dark integumental background, appressed except for bristling genal beard; integuments subimpunctate.

Head with moderately prominent eyes of about 40 facets; lateral vertexal carinae well developed; vertex convex between the two nude, deep vertexal foveae; interfoveal sulcus defined near foveae but broadly evanescent and confused apically, this sulcus appearing as a broken, inverted U in some lights and as an inverted V in others; front gently declivous between antennal tubercles, this area confused and weakly scabro-punctate and with well defined lateral margins over antennal acetabulae but broadly united with clypeal area medianly; clypeal area more declivous and distally granulate-punctate, bearing a median longitudinal carinoid tumulus from apical clypeal margin for apical half of clypeal area.

Antennae with segment X not foveate on ventral face; segment XI large, ventral face slightly flattened and bearing a weak foveoid scar.

Pronotum with median discal sulcus extending over disc for the basal three-fourths of discal length.

Elytra with inconspicuous sloped humeri; each elytron trifoveate near base, with weak sutural stria and weak discal impression for basal third of elytral length; flank of elytron bearing a poorly developed subhumeral fovea and subepipleural sulcoid impression.

Abdomen with five visible tergites in a median length ratio of 4.0/2.8-2.0/2.5/2.0 with first bearing a pair of basal abdominal carinae that are one-fifth as long as segment and separated by 22 percent of segmental width. Sternite ratio not attempted as the aedeagus is exserted. As is usual in the subgenus *Babnormodes* the aedeagus is a very reduced plate which does not offer those bizarre features so useful in discrimination of species of *Empinodes* and *Batriasymmodes*. Legs characteristic of males of *Babnormodes*, with protibiae distally flattened and slightly contorted; mesotarsi abnormal, with the second tarsomere compressed, glabrous, translucent and ventrally notched.

Described on a single male, the type in author's collection, and collected by T. C. Barr, Jr. in Benderman Cave, near Southport, Maury County, Tennessee, on August 10, 1957.

Ferulifer is another member of the *gemmus - barri - gemmoides* group. The tenth antennomere is similar to *gemmus*, the eleventh antennomere is similar to *gemmoides* and *barri*. The frontal margin is

much more interrupted medianly than any others in the group, and *ferulifer* differs from the other three in having a rodlike carinoid tubercle from mid-clypeal margin to over half of clypeal area.

Batrisodes *(Babnormodes)* **jocuvestus** new species

Type Male. Head 0.33 mm long x 0.42 mm wide; pronotum 0.42 x 0.38; elytra 0.64 x 0.60; abdomen 0.56 x 0.53; total length 1.95 mm.

Shining reddish brown; pubescence sparse, rather long and semiappressed, except for bristling genal beard; integuments subimpunctate except for a slight microasperation at origin of each seta.

Head with moderately prominent eyes of about 40 facets; lateral vertexal carinae entire but not strongly developed; cervicum and occiput bisected by a carina that terminates between the two deep, nude vertexal foveae; this occipital carina is interrupted, and weakly formed on the convex vertexal field between the vertexal foveae; these foveae are united by an inverted U-shaped sulcus which is entire; front gently declivous between antennal tubercles, shining and sparsely microgranulate; the frontal margin is blackened and carinoid laterally over the antennal acetabulae but medianly becomes weaker, although it is entire from a direct dorsal view; clypeal area crowded micro-granulate and medianly bisected by a carinoid ridge; this clypeal ridge is more strongly formed at its origin on the apical clypeal margin, becoming lower and broader to finally merge with the angulate median point of the frontal margin; this union means that the face is weakly trisected by an inverted Y-shaped figure.

Antennae with segment X not foveate on ventral face; segment XI with ventral face slightly flattened for basal half.

Pronotum with the disc not bearing a median longitudinal sulcus.

Elytra as described for *ferulifer*.

Abdomen with five visible tergites in median length ratio of 4.0/2.0/1.6-2.5/1.4 with the first bearing a pair of basal abdominal carinae that are one-fourth as long as segment and separated by 20 percent of segmental width at tips. Five sternites visible in median length ratio of 2.7/1.0/0.7/-1.7/1.8.

Legs characteristic of males of subgenus *Babnormodes,* as noted for *ferulifer*.

Described on a single male, the type in the author's collection. Collected by Walter R. Suter in Aladdin Cave, near Maysville, Madison County, Alabama, on June 20, 1959, and given to the author by John A. Wagner.

Jocuvestus is another member of the *gemmus - barri - gemmoides* group. The combination of the trisected face, flattened eleventh and afoveate tenth antennal segments serves to separate *jocuvestus* from its allies. Furthermore, all of the group inhabit caves in Dickson County, Tennessee, except *jocuvestus* known from a single cave in Madison County, Alabama. This new cavernicole is most closely allied on external anatomy to *ferulifer* among cavernicoles, and to *Babnormodes appalachianus* Casey among the epigean fauna (Park, 1947).

Batrisodes *(Babnormodes)* **clypeospecus** new species

Type Male. Head 0.45 mm long x 0.42 mm wide; pronotum 0.42 x 0.42; elytra 0.64 x 0.64; abdomen 0.60 x 0.60; total length 2 mm.

Shining reddish brown, with flavous, moderately long and abundant pubescence which is semiappressed except for bristling genal beard; integuments subimpunctate except for face.

Head with moderately prominent eyes of about 32 facets; lateral vertexal carinae poorly developed; short occipital carinae poorly developed; vertex tumid between the two deep, nude vertexal foveae; inverted U-shaped interfoveal sulcus broadly interrupted apically; vertex external to the interfoveal area coarsely punctate, the antennal tubercles especially so, with each having about nine very coarse punctures; face declivous and unmodified, with the dorsal or frontal area coarsely punctate and the ventral or clypeal area microgranulate. This clypeal area is diagnostic: the clypeus narrows distally to form the narrow clypeo-labral suture; immediately posterior to this suture the clypeus is laterally expanded and dorsoventrally thickened, with subacute lateral angles; this thickened area bears a slightly raised biarcuate margin, with the two arcuations uniting medianly in a thin small lobe. This is best studied from a direct facial view.

Antennal with segments X and XI very large; X as wide as eleventh, with flattened ventral face bearing a large fovea, this fovea about three-fourths as long and as wide as segment, its orifice fringed with a ring of setae, and the fovea deeper mesially than laterally; XI with ventral face flattened, not bearing a spine or tooth.

Pronotal disc bisected by a faint longitudinal sulcoid impression to apical four-fifths of pronotal length.

Elytra as described for *ferulifer*. Metathoracic wings present.

Abdomen with five visible tergites in median length ratio of 4.0/2.0/1.7-1.6/1.6 with last vertical; first tergite with a pair of basal abdominal carinae that are one-fourth the segmental length and separated by one-fourth of total segmental width. Width length ratio of five visible sternites not obtained as a consequence of the exsertion of aedeagus. Legs characteristic of the subgenus *Babnormodes,* as noted for *ferulifer.*

Aedeagus characteristic of the subgenus *Babnormodes,* consisting of a translucent, elongate plate which is concave distally, with the distal margin rounded-truncate and bearing a distally-directed cusp at center or displaced to the right or left of center. The intraspecies differences are small and the aedeagus is not the important taxonomic feature of *Batriasymmodes* and *Empinodes*. The aedeagus of *clypeospecus* has the distal cusp slightly to the morphological left of center; this organ measures in the type male 0.268 mm long, 0.140 mm at distal (morphological posterior) end and 0.100 mm at proximal (morphological anterior) end.

Female as for male except that (1) eyes are rudimentary of 18 facets; (2) lateral vertexal carinae are rudimentary to absent and interfoveal sulcus more nearly entire, only narrowly interrupted apically; (3) clypeal marginal biarcuation less pronounced and with median point less evident; (4) antennal club more obviously of last three segments, X not much wider than IX, and slightly narrower than XI, with tenth and eleventh not unusually large and neither flattened nor foveate beneath; (5) legs with protibiae not distally expanded or contorted, and mesotarsi simply cylindrical.

Described on eight males and thirteen females, type and twenty paratypes collected by Thomas C. Barr, Jr. on March 7, 1959 in Reed

Creek Cave, Fentress County, Tennessee. A pair in the collection of Dr. Barr, a pair in the collection of Mr. Steeves, type and sixteen paratypes in author's collection.

The median lobe of the clypeal margin is present in both sexes, and varies from a short rounded contour in the type specimen to a more pronounced lobe medianly everted into a small acute tooth.

At the median portion of the clypeus between the clypeal margin and the clypeolabral suture a small tubercle is often present and varies from absent to obvious.

One of the female paratypes was heavily infested with a fungus. Mycelial branches and what appeared to be fruiting bodies arose from the elytral suture. In general appearance this fungus looked like the ascomycete genus *Stilbum*.

On structural grounds, the nearest ally of *clypeospecus* would appear to be *Batrisodes specus* Park (1951:35) in the subgenus *Babnormodes*. The aedeagei and male antennal structure are very similar but there is an obvious difference in the face. The clypeal margin of *specus* is blackened, thin, directed distally and is in the form of a broadly rounded arcuation in both sexes.

In addition to the type series from Reed Creek Cave, Fentress County, there is a series collected by Harrison R. Steeves, Jr. on September 10, 1959, of two males under rock in Upper Parrott Cave and a male and female under rock in Lower Parrott Cave, in adjoining Overton County, Tennessee. Two specimens in the collection of Mr. Steeves.

Batrisodes *(Babnormodes)* **pannosus** new species

Type Male. Similar in size, color, pubescence and general external anatomy to *clypeospecus*, but differing in the following ways.

The face is sparsely microgranulate; front steeply declivous and clypeus lengthily declivous; where front and clypeus merge the clypeus is longitudinally carinoid each side of the union; clypeal margin is definitive, dark in color with the edge very roughly and irregularly crenulate-granulate; inverted U-shaped interfoveal sulcus uniting two deep, nude vertexal foveae is entire and obvious.

Described on five specimens (three males and two females) all collected by Thomas C. Barr, Jr., in Pedigo Cave (also known as Wall Cave). The type and three paratypes in the author's collection, one paratype in collection of Dr. Barr. Type collected October 4, 1959, and paratypes collected December 5, 1959.

The type locality lies about two miles north of Cookeville, Putnam County, Tennessee. The cave drainage is probably Blackburn Fork of Roaring River, thence into the Cumberland River.

Of especial importance is the discovery that the *pannosus* population exhibited dimorphism among the males. Both sexes had a rather poorly developed subhumeral fovea, and the ocular facet number was typical of the subgenus, with the females having reduced eyes of 14 to 18 facets and the males of 34 to 36 facets. One of the males (the type) had antennal segment X swollen and bearing a large fovea on

the ventral face, as in *clypeospecus* (*dimorphic major form*), whereas the other two males had an unmodified, female-like antennal segment X (*dimorphic minor form*). In other respects, such as the subgenerically modified protibiae and mesotarsi, these minor males were typical. All of the five specimens had the definitive clypeal carina.

Batrisodes *(Babnormodes)* tumoris new species

Type Male. Head 0.42 mm long x 0.42 mm wide; pronotum 0.39 x 0.37; elytra 0.64 x 0.64; abdomen 0.60 x 0.56; total length 2 mm.

Shining reddish brown; pubescence rather long, golden, semiappressed, except semierect on vertexal tumidity, and bristling genal beard; integuments punctulate to subimpunctate, except for a few broad, shallow punctures on face.

Head with rather prominent eyes of about 32 facets; lateral vertexal carinae thin but present; median vertexal carina obsolescent; pair of nude vertexal foveae with a faint sulcoid impression from each fovea, the external margin of which is just discernible, whereas the internal sulcal wall is obsolescent; these two foveal impressions do not unite anteriorly; vertex between the foveae and sulcoid impressions medianly tumid, this glabrous tumidity extending apically where it merges with the face in a simple, steeply declivous field, there being no frontal margin separating front from clypeus; the frontal or dorsal part of the face bears a few very large but shallow punctures, the face then narrows between antennal acetabulae and becomes just discernibly transversely impressed; ventral to this faint impression the clypeal area is seen to be microreticulate to the evenly rounded, subogival clypeal margin.

Eleven-segmented antennae distantly articulated as usual, with a club of the last three segments; segments X and XI subequal in width; X with the ventral face bearing a large fovea; this fovea *per se* is deep, circular and its orifice fringed with a row of inwardly directed setae; the mesial wall of the fovea is thrown into a defined rim but the lateral wall fades into a general depression; the fovea has a diameter of two-thirds the length of the segment, and the general depression noted is about four-fifths the segmental length; XI with the ventral face flattened-arcuate for about the basal three-fourths of segmental length.

Pronotum with the median discal sulcus absent as such, a just discernible trace of the impression in basal fourth of disc.

Elytra as described for *ferulifer*.

Abdomen with five visible tergites in median length ratio of 4.0/1.7/1.6/-2.5/1.5 with first tergite bearing a pair of well formed basal abdominal carinae that are one-fourth as long as segment and separated by 23 percent of total segmental width; last tergite vertical, simple with strongly and evenly rounded posterior margin. Five visible sternites but median length ratio not studied as a consequence of extrusion of aedeagus. Aedeagus typical of subgenus, with the discal cusp acute and nearly at center of posterior margin; the internal sac has been extruded in two stages, the basal portion boletiform, as illustrated for *subterraneus* and *valentinei* (Park, 1951, figs. 7a and 8a); the distal portion of the internal sac is about half as wide and twice as long as the basal portion, coiled, cylindrical, and slightly thickened at terminus.

Legs typical of *Babnormodes* males, as noted for *ferulifer*. Female similar to male except that (1) eyes are smaller, of 14 facets; (2) head with less swollen vertex, face simply declivous bearing confused, shallow, coarse punc-

tures dorsally between antennal tubercles and becoming punctulate ventrally, but lacking the distinctive vertexal vault and clypeal reticulation of the male; (3) antennae with simple, unmodified three-segmented club; (4) fifth tergite with a more rounded-triangular distal margin; (5) simple legs, with unmodified protibiae and mesotarsi.

Described on one pair, type and paratype, in author's collection. Collected by Harrison R. Steeves, Jr. on June 21, 1959, in the twilight zone of McClusky Cave, Colbert County, Alabama, beneath a rock.

This new species fits *specus* in a recent key (Park, 1958:43) but differs radically from *specus* and *clypeospecus* in the structure of the vertex and face. Because of its capture in the twilight zone, it was thought that *tumoris* might be an undescribed epigean trogloxene, especially since the cavernicolous *valentinei* has been taken near the cave mouth of Goat Cave, the type locality, by the author in small holes of the twilight zone.

The reduced ocular facet number of the female *tumoris* suggests a true cavernicolous distribution. Among epigean species, *tumoris* is distinctive, but most closely allied to *foveicornis* (Casey) of Kentucky and Tennessee (Park, 1947:56 and 85).

Batrisodes *(?Babnormodes)* **krekeleri** new species

Type Female. Head 0.43 mm long x 0.42 mm wide through eyes; pronotum 0.43 x 0.42; elytra 0.60 x 0.67; abdomen 0.53 x 0.67; total length 2 mm.

Only moderately shining with long, flavous pubescence which is semi-appressed except for the bristling genal beard; integuments punctulate except for the head and first three sternites noted later.

Head with rudimentary eyes of 12 facets, lateral vertexal carinae blackened and well formed; vertex tumid between the two nude vertexal foveae, with a short occipital carina and just anteriad of this, at center of tumidity is a longitudinally oval impression; interfoveal sulcus broadly interrupted apically; vertex external to this area increasingly coarsely punctate apically and this vertexal area merging gradually into the coarsely punctate and lengthily declivous face; some of the median punctures of the clypeal area longitudinally strioid. Antennae unmodified.

Pronotum with basal half of disc bearing a broad, poorly defined and just discernible longitudinal sulcoid impression.

Elytra as described for *ferulifer*.

Abdomen with five visible tergites in median length ratio of 4.4/2.0/1.5/-2.5/1.0 with last tergite vertical; first tergite with a pair of basal abdominal carinae which are 22 percent as long as segment and separated by 20 percent of segmental width. Five visible sternites in median length ratio of 2.0/1.0/-0.8/0.8/2.0 with the first three sternites coarsely, confusedly punctate and the second and third sternites not flat medianly but with the apical half distinctly and progressively turned ventrally.

Legs slightly heavier than usual with each metatibia bearing an apical pencil of setae.

Described on one female, the type in author's collection. This unique collected by Carl H. Krekeler, in whose honor this species is named, and W. Bloom on August 3, 1959, in Cave Spring, two and

one-half miles south-southwest of New Washington, Clark County, Indiana.

The sex of the specimen precludes definite assignment to subgenus. Its present position in *Babnormodes* will probably stand, and when the male sex is discovered assignment can be made easily. There are only two Nearctic subgenera which are known to contain cavernicoles. *Excavodes* includes a single cavernicole, *cavernosus* Park (1951:25) from Butler County, Alabama, and the female of this species has an entirely different face. *Babnormodes* includes many cavernicoles.

Of species of cavernicolous *Babnormodes* where the female sex is known, allied species are *henroti, gemmus* and *barri*. All three of these have the first three tergites impunctate to punctulate; *gemmus* and *barri* have the second and third sternites flat medianly but *henroti* has the posterior half of these sternites very slightly turned ventrally. Therefore, *krekeleri* would seem to be most closely allied to *henroti* on the basis of present information; *henroti* Park (1956-70), is known from the type locality of Vance Cave, near Park City, Barren County, Kentucky, as well as Beckton Cave, near Park City, Barren County, and White Cave, Edmonson County, Kentucky; also from Radio Room of Mammoth Cave in the Barren County section of this large cavern with Green River drainage (cf. Park, 1958:45-46).

The question whether *krekeleri* might be an undescribed epigean species which had wandered in Cave Spring was easily discarded on present information. Epigean females of *Batrisodes* have been keyed where this sex is known (Park, 1947:62); *krekeleri* cannot fit the first key couplet as epigean species of *Batriasymmodes* are the only ones in which the female sex has rudimentary eyes, but all members of this subgenus lack metatibial spurs.

This is the first cavernicolous pselaphid known from Indiana.

Batrisodes schneiderensis new species

Type Female. Head 0.42 mm long x 0.45 mm wide; pronotum 0.44 x 0.47; elytra 0.67 x 0.74; abdomen 0.60 x 0.67; total length 2.1 mm.

Shining reddish brown; flavous pubescence subprostrate. Integuments as follows: entire vertex, except interfoveal sulcus, as well as face coarsely punctate; ventral surface of head coarsely, cribrately punctate; anterior fourth of pronotum and median first half of disc coarsely punctate; elytra sparsely but distinctly punctate; tergites more sparsely but distinctly punctate, the punctures becoming weaker and more sparse posteriorly; fifth visible sternite sparingly coarsely punctate.

Head with moderately prominent eyes of about 22 facets; a pair of perforate, nude, deep vertexal foveae connected by an entire, deep inverted U-shaped sulcus which is in sharp relief as a consequence of the punctation described previously; lateral vertexal carinae not evident but median vertexal carina black and strongly formed from base of occiput nearly to interfoveal sulcus; this interfoveal area flattened, not tumid; face declivous and simple, other than punctation.

Antennae distantly articulated and eleven-segmented as usual, with simple, three-segmented club which is unmodified and typical of females.

Pronotum with median longitudinal discal sulcus to anterior fourth, this impression distinct as a consequence of punctate condition noted previously.

Elytra with oblique, rather obvious, rounded humeral angles; each elytron with three nude antebasal foveae, obvious sutural stria and weak discal impression for basal third of length; flank with subhumeral fovea and subepipleural sulcus.

Abdomen with five visible tergites in median length ratio of 4.5/2.4/1.5-2.5/1.4 with first bearing a pair of strong, cuneiform basal abdominal carinae that are between a fourth and a fifth of total tergite length and are separated at tips of about 22 per cent of total tergite width; fifth tergite vertical and medianly tumid (in certain aspects subtuberculate). Five visible sternites in median length ratio of 3.0/1.0/1.0/1.3/2.0 with last sternite punctate as noted.

Legs unmodified, with metatibiae each bearing a rudimentary and inconspicuous, tapered group of setae at apex of mesial face.

Described on an unique female, in collection of author, collected by Thomas C. Barr, Jr. and H. M. Koepke in Schneider Ranch Cave, twelve miles north-northeast of Boerne, Kendall County, Texas, on August 30, 1959.

This is a very interesting specimen from a number of points of view. It may be a trogloxene but the ocular facet number of 22 facets is unfortunate: this number is much too low for females of subgenera of *Batrisodes*. The facet number is much too high for *Batriasymmodes*. Where the female sex is known, the epigean species have been keyed out (Park, 1947:62), and *schneiderensis* is eliminated in the first key couplet on facet number. Turning to cavernicoles in this genus, the facet number is too high for this sex (Park, 1956 and 1958).

The metatibial spur also presents difficulties. This spur is absent in both sexes of *Batriasymmodes,* whether epigean or hypogean; it is present and almost always well formed in both sexes of the other subgenera, whether epigean or hypogean. In *schneiderensis* this setose spur is quite short, tapered and very inconspicuous.

Consequently, *schneiderensis* is intermediate in both ocular facet number and metatibial spurs. Finally, it cannot be placed in a subgenus until the male sex is discovered.

Bythinopsis hubrichti new species

Type Male. Head 0.27 mm long x 0.27 mm wide; pronotum 0.27 x 0.32; elytra 0.49 x 0.53; abdomen 0.37 x 0.51; total length 1.4 mm.

Moderately shining, dark reddish brown; pubescence short, sparse, semi-appressed. Integuments punctate as follows: head scabro-punctate granulate above, and sparsely but distinctively microtuberculate below; pronotum sparsely but coarsely punctate, the punctures varying from deep near base to shallow about disc and in certain lights these antebasal punctures appear to have a raised rim; elytra sparsely shallowly punctate to punctulate; tergum more finely punctulate.

Head with vestigial eyes of three facets arranged in an equilateral triangle; head rather flattened above with vertex only slightly convex in median posterior half, with antennae on a subquadrate rostrum, the sides of which curve outward to form the posterior two-thirds of head; a pair of small ver-

texal foveae, each fovea about the size of an ocular facet, placed anterior to the eyes and mutually more remote than either to its adjacent lateral margin; a subangulate interfoveal sulcus appears to be entire but this is obscured by the rough punctation alluded to previously; face short, vertical, laterally compressed and simple; labrum short, very transverse, as wide as clypeus; ventral surface of head gibbous with a transverse glabrous concavity behind mental area, the impression surrounded by the distinctive microtubercles noted previously (relatively simple for males of this genus).

Maxillary palpi four-segmented and characteristic of the genus; segment I very short; II very elongate, pedunculate, slightly arcuate and studded with microtubercles; III short, nearly cylindrical, also microtuberculate; IV longest and widest segment, densely clothed with fine, short pubescence and bearing a palpal cone obliquely at apex, the segment briefly pedunculate then rapidly, asymmetrically very elongate oval, the segment being three times longer than wide.

Antennae eleven-segmented, inserted in small but distinct tubercles at either anterior angle of the flattened rostrum; these organs 0.53 mm long; segment I relatively very elongate, 0.134 mm long; II to X inclusive 0.268 mm; XI 0.134 mm long; II as wide as first, subcircular; III-VIII subequally wide, the third obconical, the others moniliform, much narrower than second; club of last three, IX slightly wider than eighth, transverse moniliform, X much larger than ninth, transverse trapezoidal, XI as long as first, pyriform.

Pronotum punctate as noted previously, and with a rather large and deep lateral antebasal fovea each side, these two foveae connected by a deep arcuate antebasal sulcus; the antebasal sulcus and foveae not easily studied because of the rough punctation.

Elytra with obliquely rounded humeri; each elytron with two large antebasal foveae, from the inner of which extends the entire sutural stria, and the outer is associated with a vague discal impression; flank bearing a large subhumeral fovea, from the outer rim of which a carina extends posteriorly, progressively approaching the lateral elytral margin, which it joins before the posterior elytral margin is reached.

Abdomen short, narrowing rapidly, with five visible tergites in a median length ratio of 2.0/1.5/1.2/1.0/1.3 with basal abdominal carinae not apparent on first tergite; first three tergites with narrow but distinct lateral margins. Six sternites are apparently visible but their median length ratio is not feasible because of the complete extrusion of the aedeagus (Fig. 1). Typical of the tribe, the first sternite extends well behind the metacoxae and is visible throughout.

Legs rather slender, unmodified; tarsi with the second segment slightly swollen with reference to the third segment, this latter bearing a large tarsal claw and an accessory bristle.

Described on an unique male, the type in author's collection. Collected by Leslie Hubricht, in whose honor this fine species is named, on August 24, 1957, in Copelin Cave, two miles east of Millerstown, Hart County, Kentucky.

The tribe Bythinini has been revised recently [Park, 1953a:253-261, figs. A-H (Plate I), A-D (Plate II), D (Plate III)] and integrated among North American pselaphid tribes (Park, 1953b). In addition, the western genus *Pselaptrichus* (Brendel, 1889), which is most closely allied to *Bythinopsis,* has been monographed by Gordon A. Marsh and

Robert O. Schuster (Marsh and Schuster, 1954; Schuster and Marsh, 1956).

At present there are only four species of *Bythinopsis* known. Two of these are epigean. *Bythinopsis tychoides* (Brendel, 1865) known from northern, glaciated states (New York, New Jersey, Pennsylvania, Ohio, Illinois, Indiana, Wisconsin, Michigan). It is regarded as a glacial relict and its probably cryophilic populations are often abundant in bogs, especially grass tussocks among sphagnum moss. The males seem to be very uncommon. For example, in a series of 168 specimens taken by Berlese funnels from bogs in Wisconsin, Michigan, Indiana, and Illinois there was not a single male. The second epigean species, *carolinae* (Casey, 1897) is known from a few specimens from North Carolina, chiefly montane counties.

In both of these epigean *Bythinopsis* the males have elaborate gular modifications reminiscent of most *Pselaptrichus* males, and from ten to twelve ocular facets per eye. The females have unmodified gular areas, and in contrast to the usual condition among pselaphids where there is a sexual differential in eye facet number, the females of epigean *Bythinopsis* have a much higher facet number, from 20 to 30 facets per eye in *tychoides* (I do not know the female *carolinae*).

The remaining two species of *Bythinopsis* are cavernicolous: *jonesi* (Park, 1951), known from one female, from Wolf Den Cave, Colbert County, Alabama, and the new species, *hubrichti*. As noted, the gular area is not spectacularly modified in male *hubrichti* and the ocular facet number is three. Apparently, the tendency for females to have a higher facet number than males in this genus extends to the cavernicoles as well since *jonesi* female has 16 facets per eye.

If we are to generalize this situation, we can say that, on the basis of available data, there is a higher facet number in females than males, and second, that there is a reduction in facet number in both sexes in cavernicoles as contrasted to epigean populations of *Bythinopsis*.

The new species *hubrichti* is readily discriminated from the other three species in the genus. It differs from all three in facet number, in the much greater roughness and extent of the punctation, and from males of epigean forms in its simple gular area. It may well be that *hubrichti* should be placed in a new subgenus, as its aedeagus and gular area are qualitatively different. This course is not followed now as it is thought that more information is needed for such a step, especially more specimens of both sexes of *jonesi* and *hubrichti*.

Machaerites *(Speleochus)* **croceus** new species

Type Male. Head 0.42 mm long x 0.24 mm wide; pronotum 0.42 x 0.42; elytra 0.80 x 0.74; abdomen (inclined) 0.33 x 0.67; total length 1.9 mm.

Shining yellowish brown with semiappressed, flavous pubescence; integuments punctate but the punctures generally are shallow, vague, with indefinite boundaries and the surface appears quite differently with different direction of lighting.

Head elongate, truncate ovoidal (Fig. 7); eyes absent; occiput and

posterior part of vertex bisected by an impressed carina; a pair of small, nude vertexal foveae from each of which extends a narrow sulcus; these foveal sulci do not unite apically, each arcuate mesially to continue apically along the mesial wall of that part of the head that forms an antennal tubercle; these latter areas punctate-scarified, with intervening space less so, continuing between tubercles as a deeper, glabrous area; this latter area is continuous with the simple, glabrous face; lower facial margin sharp and carinoid; labrum large and transverse; left mandible crossed dorsal to right; maxillary palpi typical of genus; ventral surface of head unmodified, simply convex basally, becoming more tumid anteriorly and then concave just behind submentum.

Antennae eleven-segmented, 0.96 mm long, very slender; segment I very lengthily obconical, 0.254 mm long; segments II-VIII 0.42 mm long, second narrower than first, elongate and very slightly obconical, third to eighth narrower than second, thread-like, all elongate and subequally wide, third longest, fourth and fifth slightly shorter, and sixth to eighth slightly shorter than fifth; club of last three, with IX elongate, slightly wider than eighth, 0.067 mm, X of same length, wider, elongate-oval; XI very elongate oviform, 0.17 mm. Note that all segments are longer than wide, and that these organs are about half as long as the body.

Pronotum as long as wide, very slightly rounded-pentagonal; a weakly formed antebasal fovea each side, these foveae indistinctly connected by a transverse, weakly formed antebasal impression.

Elytra with oblique humeral angles; each elytron with a small sutural antebasal fovea at origin of sutural stria, this stria becomes obsolescent at apical five-sevenths; base of elytron punctate-scarified and disc without impression; flank unmodified, no subhumeral fovea.

Abdomen strongly inclined so that it appears very short and pyramidal from a dorsal view; five tergites visible in median length ratio of 2.0/1.8/1.3-1.7/2.0 with basal abdominal carinae not evident and narrow margins on the first three tergites; six sternites visible but median length ratio not feasible as the aedeagus is slightly extruded, the first and second sternites subequally long, third to fifth much shorter and subequally long, sixth longest, almost as long as first two united.

Legs with clavate femora, the first pair being the most tumid; protrochanters and base of ventral face of profemur with microtubercles; mesotrochanters compressed, with ventral edge carinoid; base of ventral face of mesofemur bearing a line of four or five coarse punctures; tarsi with a strong tarsal claw and an accessory setiform appendage; metatibiae internally arcuate in posterior fourth, with a short, stout spine at ventral face of apex.

Described on two males, in collection of author. Type from Lott Cave, Madison County, Alabama; other male from Twin Cave, near Brownsboro, Madison County, Alabama. Lott Cave and Twin Cave are about 1.5 miles apart, and both males were checked against the above description so that they appear to represent the same species. Unfortunately both specimens were slightly teneral so that the aedeagus was not taken out. It has been the author's experience that details of this organ are not too reliable in a teneral individual.

Machaerites *(Subterrochus)* **eurous** new species

Type Female. Head 0.37 mm long x 0.32 mm wide; pronotum 0.37 x 0.45; elytra 0.87 x 0.74; abdomen 0.42 x 0.67; total length 2 mm.

Shining dark yellowish brown with semiappressed flavous pubescence; integuments punctulate to scarified punctate, the punctures shallow, often vague and incomplete.

Head rounded subtriangular and slightly longer than wide (Fig. 8); eyes absent; occiput bisected by a short carina; a pair of nude vertexal foveae but foveal sulcoid impressions absent as such, instead the vertex medianly and anterior of these foveae is scarified and impressed, this impression deepening between the obvious antennal tubercles; on each lateral part of the orifice of the vertexal foveae the vertex is erected in a small tubercle; face simply, vertically declivous and punctate-granulate; labrum very transverse with a broadly concave distal margin; mandibles with long rami, the left of which is crossed dorsal to the right; ventral surface of head simple and unmodified, transversely gibbous near center and depressed behind submentum; maxillary palpi as for genus.

Antennae eleven-segmented, 0.93 mm long, slender; segment I very lengthily obconical, 0.20 mm long; segments II-VIII 0.42 mm long, second slightly narrower than first, elongate truncate-oval, third to eighth narrower than second, all elongate and subequally wide, third elongate obconical and longest, fourth shorter than third, fifth to eighth each shorter than fourth but elongate; club of last three, IX slightly wider and longer than eighth, elongate oval, 0.067 mm long, X of same length, slightly wider than ninth, nearly quadrate oval, XI elongate oviform, 0.17 mm.

Pronotum wider than long, rounded pentagonal, with a distinct antebasal fovea each side, these connected by a distinct antebasal sulcus.

Elytra with obliquely rounded humeri; each elytron with a distinct sutural antebasal fovea, a vague foveoid impression at humeral position, a strong sutural stria that becomes evanescent at apical five-sevenths, flank unmodified, no subhumeral fovea.

Abdomen strongly inclined, appearing short and pyramidal from a dorsal view; five visible tergites in median length ratio of 2.3/2.0/1.8/1.7/1.6 lacking basal abdominal carinae on first, and first three with lateral margins; six visible sternites in median length ratio of 1.5/2.0/0.6/0.4/0.6/1.0 with first typical of tribe in being longer than metacoxae and visible from side to side.

Legs with profemora slightly inflated and other femora progressively much less so; protrochanters and base of ventral face of profemora with microtubercles; mesotrochanters not unusually compressed and ventral face rounded, not carinoid; metatibiae straight, not distally spined; tarsi with a large claw and a distinct setiform appendage.

Described on an unique female, the type, in the collection of the Alabama Museum of Natural History. Collected by Walter B. Jones on May 10, 1959, in Jess Elliot Cave, Jackson County, Alabama.

This new species is easily discriminated. The tubercle on the lateral rim of each vertexal fovea is, so far, unique in the genus, not being present in any described population of *Speleochus* and *Subterrochus* except *eurous.* In addition, the well-marked sutural antebasal elytral fovea will separate it from known species except *croceus.*

Machaerites *(Subterrochus)* **steevesi** new species

Type Male. Head 0.33 mm long x 0.30 mm wide; pronotum 0.36 x 0.37; elytra 0.53 x 0.62; abdomen 0.33 x 0.60 inclined; total length 1.5 mm.

Shining, orange brown with rather short suberect, flavous pubescence; integuments differentially sculptured; head sparsely microgranulate; pronotum subimpunctate; elytra with coarse but shallow punctures and tergum similar but punctures more indefinite.

Head longer than wide, broadly subtruncate apically to give a truncated pyriform outline (Fig. 4); eyes absent; cervicum and base of occiput bisected by a carina; pair of nude, rather large, perforate vertexal foveae near base of sparsely microgranulate, apically deepening impression which separates the rather sharply defined antennal tubercles and is continuous with the simple, declivous, microgranulate face; labrum slightly transverse; left mandible crossed dorsal to right; gular area deeply excavated and the basal rim of this excavation strongly modified (Fig. 6); maxillary palpi as for genus.

Antennae eleven-segmented, 0.8 mm long; segment I lengthily obconical, 0.20 mm long; segments II-VIII 0.33 mm long, second hardly narrower than first, elongate truncate-oval, third to eighth obviously narrower than second, third longest, lengthily obconical, third to sixth subequally wide, seventh and eighth submoniliform with length and width subequal; club of last three, IX 0.67 mm long, suddenly wider than eighth, elongate oval; X same length as ninth, subspherical; XI elongate oviform, 0.15 mm long.

Pronotum almost subquadrate, rounded pentagonal; small, nude, perforate antebasal fovea each side, these foveae faintly connected by a just discernible transverse antebasal sulcoid impression.

Elytra with obliquely rounded humeri; each elytron with a distinct humeral fovea at origin of a discal impression which extends through basal fourth of length, sutural stria not evident; flank unmodified, no subhumeral fovea. Metathoracic wings absent.

Abdomen strongly inclined, appearing short and pyramidal from a strictly dorsal viewpoint; five visible tergites in median length ratio of 2.0/1.5/1.4/-1.3/1.3 with basal abdominal carinae not evident and first three tergites with distinct, narrow margins. Six visible sternites, lengths substantially as for *eurous* but ratio not practicable as aedeagus is partially extruded.

Legs with protrochanters and base of ventral face of profemora microtuberculate; profemora modestly clavate, other femora progressively less so; mesotrochanters with ventral face convex and only slightly subcarinoid toward base, in sharp contrast to those of *croceus* male *vide supra;* tarsi with a strong tarsal claw and a shorter, stout accessory setiform appendage; metatibiae slender, almost straight, without an apical spine.

Described on three males from Guffey Cave, Marshall County, Alabama. Type on January 17, 1959, and two paratypes on March 22, 1959. Collected by Harrison R. Steeves, Jr., beneath rock in twilight zone of cave. Type and second paratype in Mr. Steeves' collection, first paratype in collection of author. This species named in honor of its collector.

The aedeagus is illustrated (Fig. 9), 0.227 mm long by 0.160 mm wide. Its general structure is that of *Subterrochus,* with the four pair of distal setae (Fig. 12).

Batriasymmodes new genus

Genotype: *Batriasymmodes monstrosus* (LeConte)

Batriasymmodes was proposed as a new subgenus of *Batrisodes* by Park (1951:11) for epigean and cavernicolous populations which had a distinctive external anatomy and basically different aedeagus.

In this same report five additional subgenera were proposed, *e.g., Babnormodes, Pubimodes, Excavodes, Elytrodes,* and *Declivodes.*

In a generic revision later (Park, 1953b:315), two additional subgenera of *Batrisodes* were proposed, *e.g., Spifemodes* and *Empinodes.*

Of these eight subgenera, all had relatively simple aedeagei with the exception of *Batriasymmodes* and *Empinodes.* The subgenus *Empinodes,* the populations of which are restricted to the Pacific Northwest as far as is known (British Columbia, Idaho, Washington, Oregon, and northern California), has been discussed recently (Park and Wagner, 1960).

Batriasymmodes has a complex, bilaterally asymmetrical aedeagus with a movable arm, and the structural details of this organ are species specific. In addition, *Batriasymmodes* differs from all of the other seven subgenera in that both sexes lack metatibial spurs of setae.

In view of the lack of metatibial spurs in combination with a distinctively different organization of the male copulatory apparatus, *Batriasymmodes* is elevated to full generic status. The epigean populations have been discussed previously (Park, 1947:56-64, 66-70 and 97-100), and the cavernicolous populations have been described (Park, 1951, 1956). The type of the subgenus, *Batrisus monstrosus* LeConte, 1850, now becomes the genotype.

The erection of the new genus necessitates the following changes in nomenclature:

Batriasymmodes troglodytes new combination

Synonym: *Batrisodes troglodytes* Park, 1951, p. 23.

Batriasymmodes spelaeus new combination

Synonym: *Batrisodes spelaeus* Park, 1951, p. 16.

Batriasymmodes quisnamus new combination

Synonyms: *Batrisodes quisnamus* Park, 1951, p. 20.
Batrisodes jeanneli Park, 1951, p. 21.
Batrisodes reduncus Park, 1956, p. 65.

Quisnamus was described on an unique female from Bunkum Cave (also known as Bunum Cave), Pickett County, Tennessee. The clypeus was bisected by a longitudinal carina and the pronotal disc was bisected by a longitudinal sulcus, whereas the original sample of *jeanneli,* based on two males, the type from Lindsay Williams Cave (also known as Avant Cave), Doweltown, DeKalb County, Tennessee and a paratype from Burial Cave, Flynn's Lick, Jackson County, Tennessee, lacked both clypeal carina and pronotal discal sulcus.

At the time, this divergence in structure was thought sufficient to separate the populations at the species level.

Reduncus was described on three females from Sam Lackey Cave, 1.5 miles southwest of Gallatin, Sumner County, Tennessee, collected in 1949 by W. B. Jones and J. M. Valentine. Another female was collected by T. C. Barr, March 9, 1956. These females lacked the clypeal carina and pronotal discal sulcus of *quisnamus,* but they possessed the

Table I.—The known *quisnamus* population

Cave	Nearest town	County	State	Collector	Sex of beetles ♀	♂	Aedeagus checked
Bunkum	Byrdstown	Pickett	Tennessee	T. C. Barr	2	0	
Pratt		Pickett	Tennessee	T. C. Barr	10	1	yes
Markam	Celina	Clay	Tennessee	T. C. Barr	6	4	yes
Kermit Parrott	Livingston	Overton	Tennessee	T. C. Barr	1	1	
Burial	Flynn's Lick	Jackson	Tennessee	W. B. Jones and J. M. Valentine	0	2	yes
Jared Hollow	Chestnut Mound	Putnam	Tennessee	L. Hubricht	2	0	
Piper	Monoville	Smith	Tennessee	T. C. Barr	1	1	
Piper	Monoville	Smith	Tennessee	T. C. Barr	2	2	
Skeleton	Monoville	Smith	Tennessee	T. C. Barr	3	4	yes
Lindsay Williams	Doweltown	DeKalb	Tennessee	L. Hubricht	3	1	yes
Cripps Mill	Smithville	DeKalb	Tennessee	T. C. and C. K. Barr	10	0	
Cripps Mill	Smithville	DeKalb	Tennessee	T. C. Barr	1	0	
Taylor Herring	Lascassas	Rutherford	Tennessee	T. C. Barr	3	1	
Sam Lackey	Gallatin	Sumner	Tennessee	W. B. Jones and J. M. Valentine	3	0	
Sam Lackey	Gallatin	Sumner	Tennessee	T. C. Barr	1	0	
Sam Lackey	Gallatin	Sumner	Tennessee	T. C. Barr	1	1	yes
Stone's River	Donelson	Davidson	Tennessee	T. C. Barr and T. S. Treanor	1	0	
Walker Spring		Wayne	Tennessee	T. C. Barr	4	3	yes
Walker Spring		Wayne	Tennessee	T. C. Barr	1	0	
Brumley	West Point	Lawrence	Tennessee	T. C. Barr	1	0	
Ann White	Keystone	Macon	Tennessee	T. C. Barr	1	0	
Hoy	Franklin	Simpson	Kentucky	L. Hubricht	1	2	yes
Steele	Franklin	Simpson	Kentucky	T. C. Barr	2	0	

lateral clypeal carinae which were lacking in *jeanneli* but present in *quisnamus*.

Dr. Barr collected a male and female from Sam Lackey Cave on December 31, 1959 — the first male from this cave to be reported. The male was a perfect *quisnamus,* hence as postulated by Park, (1958:45), *reduncus* becomes a synonym of *quisnamus*.

The reasons for synonymising *jeanneli* included a critical study of ten females from Pratt Cave, in Pickett County, not far from the type locality of *quisnamus* in Bunkum Cave, Pickett County. It will be remembered that the unique type of *quisnamus* has a clypeal carina and a pronotal discal sulcus, whereas *jeanneli* had neither clypeal carina nor pronotal discal sulcus. The ten females from Pratt Cave had the following distribution of these characters: five had the clypeus bisected by a longitudinal carina and the pronotal disc bisected by a longitudinal sulcus; two had no clypeal carina but did have the pronotal sulcus; one had the clypeal carina but no pronotal sulcus; two had neither clypeal carina nor pronotal sulcus. Therefore these two characters varied from absent to present independently, from a "quisnamus" to a "jeanneli" condition. Finally, the single male from Pratt Cave had the aedeagus of *jeanneli,* and consequently *quisnamus* became the valid name by page priority.

Table I lists the known *quisnamus* population at the present time.

CHECKLIST OF CAVERNICOLOUS FORMS

Tribe BATRISINI Raffray, 1890
Subtribe AMAUROPSINA Jeannel, 1949
Genus *Arianops* Brendel, 1893
Subgenus *Arispeleops* Park, 1951

Arianops (*Arispeleops*) *cavernensis* Park, 1951, p. 41.
Type locality.—Saltpetre Cave, Marshall County, Alabama.
Arianops (*Arispeleops*) *jeanneli* Park, 1956, p. 85.
Type locality.—Gilly's Cave, Pennington Gap, Virginia.
Arianops (*Arispeleops*) *stygica* new species
Type locality.—Cumberland Caverns, Warren County, Tennessee.

Subtribe BATRISINA Jeannel, 1948
Genus *Batrisodes* Reitter, 1881
Subgenus *Excavodes* Park, 1951

Batrisodes (*Excavodes*) *cavernosus* Park, 1951, p. 25
Type locality.—Hinson Cave, Greenville, Butler County, Alabama.

Subgenus *Babnormodes* Park, 1951

Batrisodes (*Babnormodes*) *profundus* Park, 1956, p. 68
Type locality.—Turk's Cave, Brooklyn, Conecuh County, Alabama.
Batrisodes (*Babnormodes*) *jonesi* Park, 1951, p. 27
Type locality.—Little Bear Cave, Tuscumbia, Colbert County, Alabama.
Batrisodes (*Babnormodes*) *barri* Park, 1958, p. 40
Type locality.—Dickson Cave, Dickson, Dickson County, Tennessee.
Batrisodes (*Babnormodes*) *subterraneus* Park, 1951, p. 30

Type locality.—Griffith Cave, Guntersville, Marshall County, Alabama.

Batrisodes (*Babnormodes*) *tumoris* new species

Type locality.—McClusky Cave, Colbert County, Alabama.

Batrisodes (*Babnormodes*) *specus* Park, 1951, p. 35

Type locality.—Hutton Cave, Sharp's Cove, Madison County, Alabama.

Batrisodes (*Babnormodes*) *clypeospecus* new species

Type locality.—Reed Creek Cave, Fentress County, Tennessee.

Batrisodes (*Babnormodes*) *pannosus* new species

Type locality.—Pedigo Cave, Cookeville, Putnam County, Tennessee.

Batrisodes (Babnormodes) hubrichti Park, 1958, p. 41

Type locality.—Beckton Cave, Beckton, Barren County, Kentucky.

Batrisodes (*Babnormodes*) *henroti* Park, 1956, p. 70

Type locality.—Vance Cave, Park City, Barren County, Kentucky.

Batrisodes (*Babnormodes*) *valentinei* Park, 1951, p. 32

Type locality.—Goat Cave, Keel Mountain, Madison County, Alabama.

Batrisodes (*Babnormodes*) *jocuvestus* new species

Type locality.—Aladdin Cave, Maysville, Sharp's Cove, Madison County, Alabama.

Batrisodes (*Babnormodes*) *ferulifer* new species

Type locality.—Benderman Cave, Southport, Maury County, Tennessee.

Batrisodes (*Babnormodes*) *gemmoides* new species

Type locality.—Columbia Caverns, Dickson County, Tennessee.

Batrisodes (*Babnormodes*) *gemmus* Park, 1956, p. 71

Type locality.—Jewel Cave, Dickson, Dickson County, Tennessee.

Batrisodes (*Babnormodes* ?) *krekeleri* new species

Type locality.—Cave Spring, New Washington, Clark County, Indiana.

Batrisodes (Babnormodes ?) schneiderensis new species

Type locality.—Schneider Ranch Cave, Boerne, Kendall County, Texas.

Genus *Batriasymmodes* new genus

Batriasymmodes troglodytes new combination

Type locality.—Rock Cave, Greenville, Butler County, Alabama.

Batriasymmodes spelaeus new combination

Type locality.—Bangor Cave, Bangor, Blount County, Alabama.

Batriasymmodes quisnamus new combination

Type locality.—Bunkum Cave, Byrdstown, Pickett County, Tennessee.

Tribe BYTHININI *sensu* Jeannel, 1949

Subtribe MACHAERITINA Jeannel, 1950

Genus *Bythinopsis* Raffray, 1908

Bythinopsis jonesi Park, 1951, p. 43

Type locality.—Wolf Den Cave, Maud, Colbert County, Alabama.

Bythinopsis hubrichti new species

Type locality.—Copelin Cave, Millerstown, Hart County, Kentucky.

Genus *Machaerites* Miller, 1885

Subgenus *Speleochus* Park, 1951

Machaerites (*Speleochus*) *stygicus* Park, 1951, p. 47

Type locality.—Toll Gate Natural Well, Monte Sano, Madison County, Alabama

Machaerites (*Speleochus*) *synstygicus* Park, 1956, p. 64

Type locality.—Barclay Cave, King Mountain, Madison County, Alabama.

Machaerites (*Speleochus*) *croceus* new species

Type locality.—Lott Cave, Madison County, Alabama.

Subgenus *Subterrochus* new subgenus

Machaerites (*Subterrochus*) *ferus* Park, 1951, p. 49
Type locality.—Aladdin Cave, Maysville, Sharp's Cove, Madison County, Alabama.

Machaerites (*Subterrochus*) *eurous* new species
Type locality.—Jess Elliot Cave, Jackson County, Alabama.

Machaerites (*Subterrochus*) *steevesi* new species
Type locality.—Guffey Cave, Marshall County, Alabama.

Tribe Speleobamini Park, 1951
Genus *Speleobama* Park, 1951

Speleobama vana Park, 1951, p. 53
Type locality.—McClunney Alabama Caverns, Clay, Jefferson County, Alabama.

KEYS TO TAXA

The following keys are devised to discriminate the described populations of North American cavernicolous pselaphid beetles, and supersede previous keys to this fauna by the author.

KEY TO TRIBES

1 Abdomen with lateral margins absent, the segments in the form of undivided rings; one or more of the first three visible segments bearing one or two entire or incomplete lateral carinae .... Batrisini, p. 86
Abdomen with narrow to broad margins on each side of the first two or three visible segments 2

2 (1) Occipito-cervical region of the head wholly covered on all sides and obscured by a conspicuous ruff of long setae; third (penultimate) segment of maxillary palpi very slender and elongate .... Speleobamini, p. 93
Occipital-cervical region of head with ruff absent; third (penultimate) segment of maxillary palpi short, as wide as long, or nearly so .... Bythinini, p. 89

Tribe BATRISINI
Key to Genera

1 Eyes absent, often replaced by a conical spine or tumulus; tarsi with a large tarsal claw and a just discernible setoid accessory claw which can be easily overlooked; very uncommon .... *Arianops*
Eyes always present but may be reduced in facet number, especially in females, where these organs may have as few as six facets; tarsi with two very unequal claws, but both distinct 2

2 (1) Metatibia with a distal, terminal bundle or spur of setae, these setae usually long, pencil-like, and of equal length, but may be short and the bundle tapering to a point; abundant .... *Batrisodes*
Metatibia lacking a pencil of setae .... *Batriasymmodes*

Genus *Arianops*

All cavernicolous species belong in the subgenus *Arispeleops*.

1 Pronotum with six baso-lateral foveae (as in the epigean species in the subgenus *Arianops*), *e.g.*, one on each side of median point of

base, one each side at lateral third, and one each side intermediate between these two .... *stygica* new species
Pronotum not having six baso-lateral foveae 2
2 (1) Pronotum with a minute, just discernible fovea each side at lateral third .... *jeanneli* Park, 1956
Pronotum lacking foveae .... *cavernensis* Park, 1951

Genus *Batrisodes*

Key to Cavernicolous Subgenera

1 Males with mesotarsi relatively simple, the second tarsomere compressed or subcylindrical, glabrous or pubescent, but not notched on ventral side near base (Fig. 14) .... *Excavodes*
Males with mesotarsi peculiarly modified, the second tarsomere always glabrous, compressed, translucent and distinctly notched near base of ventral face (Fig. 13) .... *Babnormodes*

Subgenus *Excavodes*

There is but one known species of this subgenus which is cavernicolous, *cavernosus* Park, 1951. The sexes may be separated as follows:

1 Male with about forty ocular facets per eye, antennal segment X subspherical, slightly wider than XI and with a small fovea (about the diameter of an ocular facet) at extreme base of ventral face .... Males
Vestigial eyes, of about fourteen ocular facets per eye; antennal segment X obviously narrower than XI and not foveate on ventral face .... Females

Subgenus *Babnormodes*

1 Male with antennal segment XI (distal segment) bearing a conspicuous oblique spine at basal margin of ventral face .... *profundus* Park, 1956
Male with antennal segment XI not as described 2
2 (1) Antennal segment X bearing a fovea on the ventral face 3
Antennal segment X not foveate on ventral face 9
3 (2) Face with front triangularly declivous to within a short distance of clypeal margin, where the apex of this frontal triangle ends abruptly in an everted transverse tubercular lamina .... *jonesi* Park, 1951
Face not as described 4
4 (3) Face with frontal margin flat, arcuate, strongly carinoid except at center where it becomes continuous with the subvertical clypeus, the clypeus with a small tubercle at center .... *barri* Park, 1958
Face simple, unevenly declivous, not tuberculated 5
5 (4) Fovea of antennal segment X relatively small (one-third the length of ventral face of segment), circular and nude .... *subterraneus* Park, 1951
Fovea of antennal segment X relatively large (three-fourths the length of ventral face of segment), in a transversely ovoidal impression, and with the foveal orifice radially setose 6
6 (5) Vertex medianly strongly tumid between vertexal foveae and distally between the widely interrupted foveal impressions, this glabrous tumidity extending apically to merge with the face in a simple, steeply declivous plane .... *tumoris* new species
Vertex not as described 7

7 (6) Clypeus erected into a transverse carina relatively near the clypeo-labral suture, this carina blackened usually from side to side, directed distally in the form of a broadly rounded arcuation; face with center of frontal declivity tending to have a small patch of short setae in a slight depression, or this depression may bear two poorly separated setose patches .... *specus* Park, 1951

Clypeus erected into a transverse carina which is relatively distant from clypeo-labral suture 8

8 (7) Clypeal carina with lateral portions usually blackened and thicker, the median area of carina usually thin; this carina biarcuate, the two arcuations meeting medianly in a small lobe or cusp .... *clypeospecus* new species

Clypeal carina blackened and roughly and irregularly crenulate-granulate-dimorphic major form .... *pannosus* new species

9 (2) Near center of facial declivity there is a pair of minute pores, each usually set in a small area of a darker color ...... *hubrichti* Park, 1958

Face not as described 10

10 (9) Near center of facial declivity there is a median minute pore, usually set in a small circular area of darker cuticle, and this area often raised in a low, convex tuberculoid field, with a pore at its ventral margin .... *henroti* Park, 1956

Face not as described 11

11(10) Face declivous on a line through antennal bases, this declivity sub-glabrous and rapidly narrowing to form a triangular field which is surrounded by the granulate-punctate clypeus; near base of this triangular field is a slightly pubescent, transversely oval impression .... *valentinei* Park, 1951

Face not as described 12

12(11) Clypeal area crowded microgranulate and bisected by a median carinoid ridge, this ridge continuing dorsally to merge with the angulate median point of the frontal margin; this gives to the face a trisected aspect .... *jocuvestus* new species

Face not trisected as decribed 13

13(12) Clypeal carina blackened and roughly and irregularly crenulate-granulate-dimorphic minor form .... *pannosus* new species

Face not as described; clypeus with a tubercle or a tuberculoid ridge 14

14(13) Clypeus bearing a median longitudinal carinoid tumulus from clypeal margin for apical half of clypeal area .... *ferulifer* new species

Clypeus not as described 15

15(14) Antennal segment XI bearing a small poroid scar or impression on its ventro-basal area .... *gemmoides* new species

Antennal segment XI not bearing such a structure .... *gemmus* Park, 1956

The above key does not include *krekeleri* new species and *schneiderensis* new species. Both of these were described on an unique female, and consequently may not be members of the subgenus *Babnormodes,* as this subgeneric allocation is made on the anatomy of the male mesotarsi. Both species, described subsequently, are distinctive anatomically and geographically. *Krekeleri* is the only cavernicolous pselaphid known north of the Ohio River, and *schneiderensis* is the only cavernicolous pselaphid known west of the Mississippi River.

Genus *Batriasymmodes*

1 Metatrochanter bearing a contorted spine; eyes relatively prominent, having from 28 to 50 ocular facets (males) 2
Metatrochanter lacking a spine; eyes vestigial or reduced, having from six to 18 ocular facets (females) 4
2 (1) Vertexal foveae pubescent; elytron bifoveate ....*troglodytes* Park, 1951
Vertexal foveae nude; elytron trifoveate 3
3 (2) Antennal segment VIII with apex of ventral face produced as an acute divergent spine; antennal segment IX simple and unmodified ....*spelaeus* Park, 1951
Antennal segment VIII with ventral face produced as a laminoid spine; antennal segment IX with ventral face irregularly concave and glabrous, with an oblique carina in basal half, and the apical half hooded by a carinoid and fimbriated margin ....*quisnamus* Park, 1951
4 (1) Vertexal foveae pubescent; elytron bifoveate ....*troglodytes* Park, 1951
Vertexal foveae nude; elytron trifoveate 5
5 (4) Last tergite medianly sulcoid with a pair of spinoidal cusps or lamina bounding this sulcus ....*spelaeus* Park, 1951
Last tergite simply convex, lacking sulcus and lamina ....*quisnamus* Park, 1951

Tribe Bythinini

Key to Genera

1 Eyes and wings absent in both sexes ....*Machaerites*
Eyes present but reduced, with males having vestigial eyes of three facets and females having sixteen facets as far as known ....*Bythinopsis*

Genus *Bythinopsis*

1 Head and pronotum shining and lightly punctulate (known from female only) ....*jonesi* Park, 1951
Head scabro-punctate granulate above and lightly microtuberculate below; pronotum sparsely, coarsely punctate, the punctures varying from deep near base to shallow about disc (known from male only) ....*hubrichti* new species

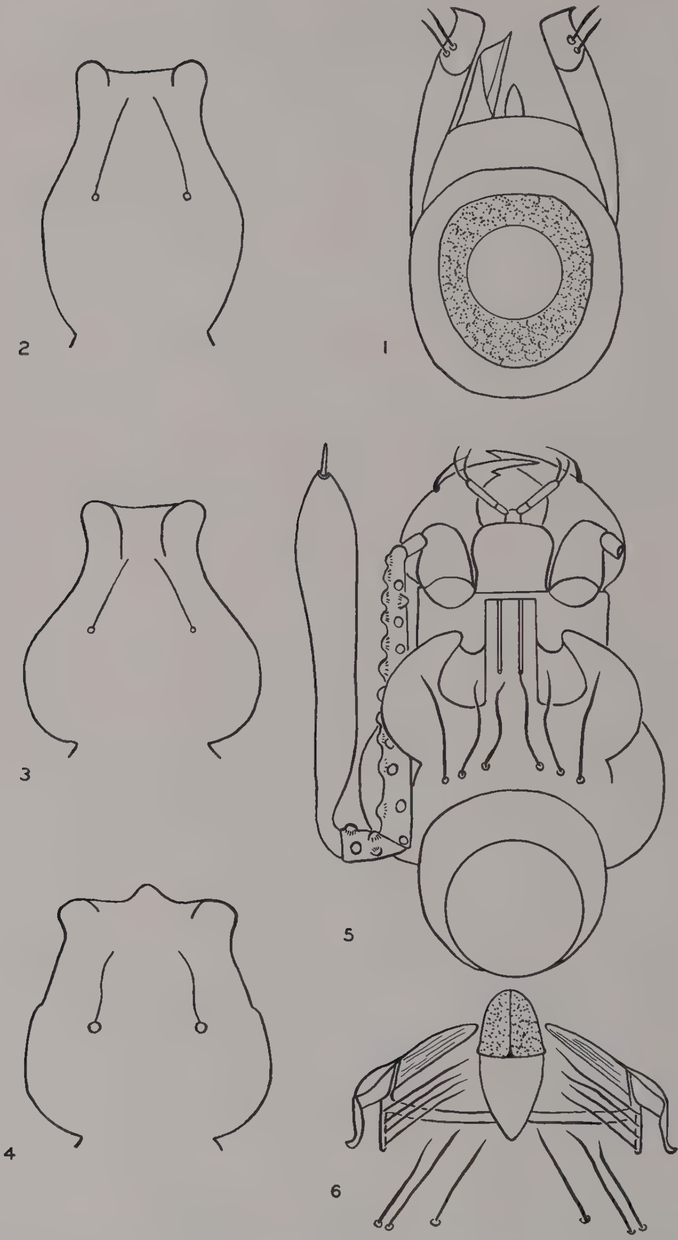
Genus *Machaerites*

Members of this genus have in common (1) simple pubescence (the setae not geminate or in pairs); (2) integuments shining (not strongly alutaceous and opaque); (3) eyes absent; (4) antennae of eleven segments; (5) second segment of maxillary palpi gradually thicker from base to apex; (6) second and (at least in American species) third segments of maxillary palpi microtuberculate.

So far as known the populations are strictly troglobiont and inhabit caves in Carniola (northeastern Italy and northwestern Yugoslavia) in Europe, and in Alabama in the United States.

Key to Subgenera

1 Each elytron with two strong, deep, large antebasal foveae; body size large, more than 2 mm long, European caves only 2
Each elytron with no trace of antebasal foveae, or with one fovea, or with vague foveoid impressions; body size smaller, not more than 2 mm; known only from caves in northern Alabama 3



Figs. 1-6.—1. *Bythinopsis hubrichti* n. sp. Aedeagus, 70×, drawn from extruded organ in type specimen. 2. *Machaerites* (*Speleochus*) *stygicus* Park. Dorsal head outline of male, 70×. 3. *Machaerites* (*Subterrochus*) *ferus* Park.

2 (1) Pronotum with a distinct transverse antebasal sulcus ....

BYTHOXENUS (Motschulsky, 1859) (one species, the subgeneric type, *subterraneus* Motschulsky, 1859 in the Grotto of Pasica, Carniola)

Pronotum with this sulcus absent ....

MACHAERITES *sensu strictiore* (one species, the subgeneric type, *spelaeus* Miller, 1855 in the Grotto of Strug, Carniola)

3 (1) Head subovoidal in dorsal outline (Fig. 2); gular area of males simply gibbous and unmodified; metatibiae of males arcuate in distal five-sevenths of length and with a terminal spine; base of elytra either wholly without foveae, or with a vague sutural impression, or with one small sutural fovea ....

SPELEOCHUS Park, 1951 (3 species known, of which *stygicus* Park, 1951 is the type of subgenus)

Head subpyriform to rounded subtriangular in dorsal outline (Figs. 3, 4); gular area of males greatly modified (Figs. 5, 6) where known; metatibiae of males straight; base of elytra either a pair of vague impressions, or with one small sutural fovea and a vague humeral impression, or with one small humeral fovea and a vague sutural impression ....

SUBTERROCHUS new subgenus (3 species known, of which *ferus* Park, 1951 is the type of this new subgenus)

Two general points should be made prior to examination of the composition of the American subgenera of *Machaerites*.

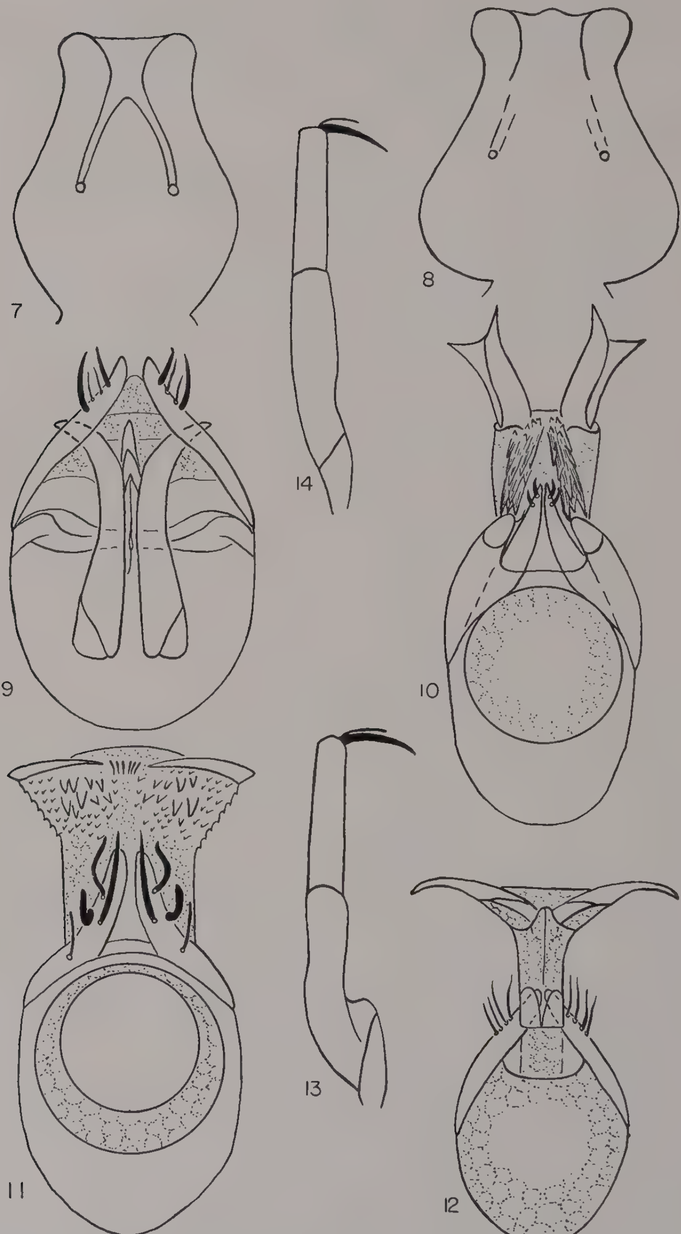
First, with accumulation of more material it is apparent that the presence or absence of an elytral fovea, or foveoid impressions is of great convenience at the species population level, but is too variable in contrast to other features to be used as a key character at the supra-species level of organization. So far, none of the American species have the two large, well formed antebasal elytral foveae of the European species, and in connection with the larger size of the Carniolian body form, may be used for the present to separate the European and American subgenera. As noted above, the qualitative differences in male secondary sex characters and the shape of the head offer more stable features for separation of American subgenera as delimited at present.

Second, the allocation of female *Machaerites* to definite species has been abandoned except in those few instances where both sexes have been taken together in the same cave niche. Consequently, earlier records (Park, 1951) are no longer considered except those from the type locality, or where males from another cave have been collected and studied.

In one case an exception has been made, an unique female having been used as the type of a new species. In this instance, the specimen was so well marked (one elytral fovea at the sutural position, and other features) that it justified description.

So far as known, the six species of *Machaerites* known from North Amer-

Dorsal head outline of male, 70×. Same scale as Fig. 2. 4. *Machaerites* (*Subterrochus*) *steevesi* n. sp. Dorsal head outline of male, 70×. Same scale as Fig. 2. 5. *Machaerites* (*Subterrochus*) *ferus* Park. Ventral view of head of male, 70×. 6. *Machaerites (Subterrochus) steevesi* n. sp. Gular area of male, 70×.



Figs. 7-14.—7. *Machaerites* (*Speleochus*) *croceus* n. sp. Dorsal head outline of male, 70×. Same scale as Fig. 2. 8. *Machaerites* (*Subterrochus*) *eurous*

ica have a restricted distribution. They are known only from caves in northern Alabama, from three adjacent counties (Madison, Jackson, and Marshall).

When additional material has accumulated and has been compared directly with the two European species in this genus it is probable that the American subgenera will be raised to full generic rank.

Subgenus *Speleochus*

1 Elytron with a fovea at origin of sutural stria ....*croceus* new species
Elytron with no antebasal foveae 2
2 (1) Aedeagus with internal sac having a pair of exsertible teeth as illustrated (Fig. 10) ....*stygicus* Park, 1951
Aedeagus with internal sac having a pair of exsertible teeth as illustrated (Fig. 11) ....*synstygicus* Park, 1956

Subgenus *Subterrochus*

1 Lateral margin of orifice of each vertexal fovea erected in a small tubercle (known from female only). ....*eurous* new species
Orifice of vertexal foveae not bearing tubercle 2
2 (1) Elytron with a fovea at humeral position; aedeagus as illustrated (Fig. 9) ....*steevesi* new species
Elytron with no antebasal foveae; aedeagus as illustrated (Fig. 12) ....*ferus* Park, 1951

Tribe SPELEOBAMINI
Genus *Speleobama*

One species known, *Speleobama vana* Park, 1951

ZOÖGEOGRAPHIC CONSIDERATIONS

In the area under study there are at least seven major drainage patterns that have been utilized presumably by cavernicolous pselaphids.

I. Southward *via* Black Warrior, Tombigbee, and Mobile Rivers into Mobile Bay.

II. Southward *via* Pigeon, Conecuh, and Escambia Rivers into Pensacola Bay.

III. Westward and northward *via* the Tennessee River into the Ohio River.

IV. Westward and northward *via* the Cumberland River into the Ohio River.

V. Westward and northward *via* the Green River into the Ohio River.

VI. Southward into the Ohio River.

VII. Southeastward *via* the Guadalupe River into the Gulf of Mexico.

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n. sp. Dorsal head outline of female, 70×. Same scale as Fig. 2. 9. *Machaerites* (*Subterrochus*) *steevesi* n. sp. Aedeagus, from slide-mount, 430×. 10. *Machaerites (Speleochus) stygicus* Park. Modified from Park, 1951. Aedeagus, from slide-mount, 430×. 11. *Machaerites* (*Speleochus*) *synstygicus* Park. After Park, 1956. Aedeagus, from slide-mount, 430×. 12. *Machaerites* (*Subterrochus*) *ferus* Park. After Park, 1951. Aedeagus, from slide-mount, 430×. 13. *Batrisodes* (*Babnormodes*). Diagram of male mesotarsus, 70×. 14. *Batrisodes* (*Excavodes*). Diagram of male mesotarsus, 70×.

A convenient initial analysis is to organize this fauna both along these seven drainages and cave habitats. This is attempted in the following table (Table II).

TABLE II.—Analysis by drainage and cave

Taxon	Number of caves inhabited	Drainage systems noted previously I	II	III	IV	V	VI	VII
Arianops								
cavernensis	1			x				
jeanneli	1			x				
stygica	1				x			
Batrisodes								
cavernosus	1		x					
profundus	1		x					
jonesi	7			x				
barri	2				x			
subterraneus	1			x				
tumoris	1			x				
specus	8			x				
clypeospecus	2				x			
pannosus	1				x			
hubrichti	1					x		
henroti	4					x		
valentinei	5			x				
jocuvestus	1			x				
ferulifer	1			x				
gemmoides	1				x			
gemmus	1				x			
krekeleri	1						x	
schneiderensis	1							x
Batriasymmodes								
troglodytes	1		x					
spelaeus	28	x(8)		x(16)	x(4)			
quisnamus	18			x(2)	x(16)			
Bythinopsis								
jonesi	1			x				
hubrichti	1				x			
Machaerites								
stygicus	3			x				
synstygicus	1			x				
croceus	2			x				
ferus	2			x				
eurous	1			x				
steevesi	1			x				
Speleobama								
vana	1	x						

TABLE III.—The known *spelaeus* population

Cave	Nearest town	County	State	Probable river drainage
Daly	Butler's Landing	Clay	Tennessee	Cumberland
Dairyhouse		White	Tennessee	Cumberland
Indian		White	Tennessee	Cumberland
McElroy		Van Buren	Tennessee	Cumberland
Indian	New Market in Jefferson County	Grainger	Tennessee	Tennessee
Bat	Shoal Creek	Lauderdale	Alabama	Tennessee
Manitou	Ft. Payne	De Kalb	Alabama	Tennessee
Thomas	Trinity in Morgan County	Lawrence	Alabama	Tennessee
Tingling Hole	Trinity in Morgan County	Lawrence	Alabama	Tennessee
Barrel	Trinity	Morgan	Alabama	Tennessee
Echols	Trinity	Morgan	Alabama	Tennessee
Ladder	Trinity	Morgan	Alabama	Tennessee
Lost Mule	Trinity	Morgan	Alabama	Tennessee
Royer	Trinity	Morgan	Alabama	Tennessee
Winchester	Trinity	Morgan	Alabama	Tennessee
Inge	Decatur	Morgan	Alabama	Tennessee
Cave Spring	Hillsboro	Morgan	Alabama	Tennessee
Kelly Ridge		Marshall	Alabama	Tennessee
Lime Point		Marshall	Alabama	Tennessee
Warrenton		Marshall	Alabama	Tennessee
Natural Bridge		Winston	Alabama	Black Warrior
Bangor	Bangor	Blount	Alabama	Black Warrior
Dixon	Brooksville	Blount	Alabama	Black Warrior
French's	Brooksville	Blount	Alabama	Black Warrior
Horseshoe	Inland	Blount	Alabama	Black Warrior
Ingram	Greystone	Blount	Alabama	Black Warrior
Posey Spring	Blountsville	Blount	Alabama	Black Warrior
McGlendon	Gallant	St. Clair	Alabama	Black Warrior

First, in terms of the seven major drainage systems the thirty-three taxa are distributed as follows: 2 in I (Black Warrior); 3 in II (Pigeon); 18 in III (Tennessee); 8 in IV (Cumberland); 3 in V (Green); 1 in VI (Ohio); 1 in VII (Guadalupe).

Of the thirty-three species only two are distributed in more than one drainage system. This lends weight to the conclusion that cavernicolous pselaphids tend to be distributed per species to a single drainage. Furthermore, the two exceptions are confined to a single genus, *Batriasymmodes*.

Second, in terms of caves occupied so far as known the thirty-three taxa are distributed as follows: 22 in one cave; 4 in two; 1 in three; 1 in four; 1 in five; 1 in seven; 1 in eight; 1 in eighteen; and 1 in twenty-eight caves.

These distributions are of interest to speleology. Twenty-two species, or roughly 67 percent of known American cavernicolous psela-

phids occupy a single cave, the type locality. For the other eleven species, four, or 12 percent, occupy only two caves, and one species, or 3 percent, occupies respectively three, four, five, seven, eight, eighteen, and twenty-eight caves.

These eleven instances in which more than one cave is occupied deserve brief attention.

Two caves occupied by one species: *Batrisodes barri, B. clypeospecus, Machaerites croceus,* and *M. ferus* each occupies a pair of caves. The distance apart of these pairs is roughly 20, 10, 2, and 5 miles respectively, and in each case the pair of caves are on the same drainage system.

Three caves occupied by one species: *Machaerites stygicus*[2] in three caves on the Flint Creek of the Tennessee River drainage, all in Madison County, Alabama.

Four caves occupied by one species: *Batrisodes henroti* in four caves in the Mammoth Cave area of Edmonson and Hart Counties of Kentucky, with Green River drainage.

Five caves occupied by one species: *Batrisodes valentinei*[3] in five caves in contiguous Jackson and Madison Counties, Alabama with Tennessee River drainage.

Seven caves occupied by one species: *Batrisodes jonesi* in seven caves clustered in western Colbert County, Alabama, with Tennessee River drainage.

Eight caves occupied by one species: *Batrisodes specus*[4] in eight caves in contiguous Madison and Marshall Counties, Alabama, with Tennessee River drainage.

The thirty-one species noted so far lend weight to the conclusion that cavernicolous pselaphids tend to occupy a single cave, or a group of caves which are relatively near one another in the same part of a drainage system.

There remain two species, again in the genus *Batriasymmodes,* which do not follow the usual pattern of either drainage distribution or cave distribution. These are *B. quisnamus,* known from eighteen caves in two drainages (Table I), and *B. spelaeus,* known from twenty-eight caves in three drainage systems. The known *spelaeus* population is listed in Table III, and the known distribution of both of these bothersome populations is suggested in Fig. 15.

These two species of *Batriasymmodes* do not follow the rule for

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[2] Distribution based now on male specimens only, and not including other records in Park, 1951.

[3] An early record (Park, 1951) of *valentinei* at Crystal Cave, Monteagle, Grundy County, Tennessee, must be rechecked, although the drainage is Tennessee River *via* Elk River. The specimen may represent a new race or species.

[4] Two early records should be rechecked (Park, 1951). These are of *specus* from Indian Cave in Grainger County, Tennessee, with Tennessee River drainage *via* Holston River, and Georgetown Cave, Georgetown, Colbert County, Alabama, with Tennessee River drainage. New races may be involved.

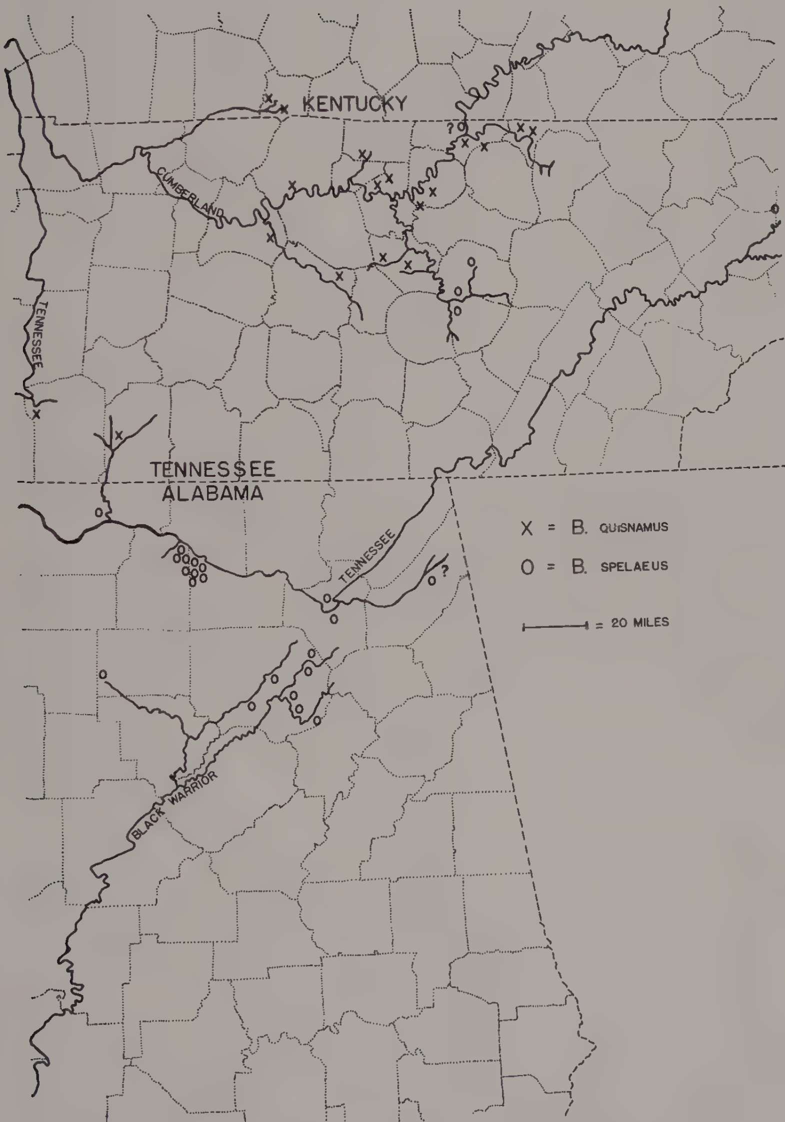

Fig. 15.—Known distribution of *Batriasymmodes quisnamus* (Park) and *Batriasymmodes spelaeus* (Park).

distribution of other known cavernicolous pselaphids, or of the cavernicolous pseudanophthalmid carabids, and rival some of the known dispersals of cave-dwelling collembolans, millepeds and phalangids.

Assuming that the collecting data were sound, the author felt that these two distribution patterns must be the result of bad taxonomy. Both species were described in 1951, and a recheck was made later (1958:44) in the case of *spelaeus* which confirmed the earlier status. Such rechecking in the case of *Batrisodes* is not promising and fortunately the latter genus did not offer such problems. In the case of *Batriasymmodes* as noted previously in this report, the aedeagus is complex and species specific, and is accompanied by species specific male antennal modifications. Furthermore in *spelaeus,* the worst offender, the female as well has a distinctive distal tergite. All subsequent efforts have reconfirmed the homogeneity of each of these populations. The question of raciation has not been studied as yet, and may assist in an eventual explanation.

Finally, of the thirty-three species so far known, only one case shows more than one species per genus in a given cave. *Batrisodes barri,* described from Dickson Cave, 1.5 miles south of Dickson, in Dickson County, Tennessee, has been collected in Columbia Caverns, Dickson County and in the latter cave, *Batrisodes gemmoides* has its type locality. These two caves are about twelve to fifteen miles apart on surface measurement, but both with Cumberland River drainage. Both *barri* and *gemmoides* are in the same subgenus, *Babnormodes,* but taxonomically occupy structurally different parts of the subgenus as based on male antennal modifications.

In general, the known cavernicolous pselaphid fauna of North America tends to occupy a single part of a drainage system, occupy a single cave, or group of caves near to one another and probably often connected by subterranean fissures, and tends to occupy a cave with either no other species of pselaphid present, or shares a cave with members of another genus of pselaphids.

Evolutionary Considerations

It would seem obvious that the only way in which epigean pselaphid stocks could become cavernicolous would be to enter caves and remain therein. After this initial intrusion, given sufficient time, isolation and selection, such stocks as survived should evolve into true cavernicoles, integrated members of the cave community, and no longer able to exist as competing epigean populations.

Apparently this course of events has taken place, but not often, and not at one time from a single ancestral stock. At present there are about 498 species of Pselaphidae in the United States, divided among 72 genera (Park 1953b, *et seq.*). These figures are under constant upward revision. The majority inhabit the deciduous forest biome of eastern North America, and include 33 species of cavernicolous pselaphids, divided among six genera.

Pselaphidae have ecological requirements and patterns of behavior

which should allow them to penetrate and colonize caves with relative ease. Most of the species live in forests. Here they inhabit the floor stratum and its numerous discontinuous extensions, *e.g.*, leaf mold, log mold, rotting sawdust mounds, tree-hole mold, tree-crotch debris, and soil. These habitat niches are all more or less dark, damp and still, relative to areas external to the forest. Where tested (Park 1929, 1947) the beetles tend to select the darker portion of a light gradient, and the moister portion of a gradient in dampness. In view of this pattern of general response it is not surprising that pselaphids should have penetrated the sod of established grasslands, the nests of ants and termites, and caves.

The night is characterized by relative darkness and dampness, and pselaphids are generally crepuscular to nocturnal. Many are dusk fliers, and come to light with increasing frequency toward the equator. All of these points suggest that the cave community would be acceptable to such pselaphid populations as could adjust to the relatively constant environment, and find sufficient food.

These beetles are to be viewed as generalized predators. In nature they feed on collembolans, mites, and fly larvae and in the laboratory can be kept on a diet of collembolans or, more conveniently, larvae of *Drosophila* (Park 1932, 1933, 1947; Engelmann, 1956). The cave biota includes all three of these arthropod orders.

It would seem that study of cavernicoles should continue to be one of the most fruitful sources of data on phylogenesis. Species of *Babnormodes* which inhabit caves form several taxonomic series, and there is some information that suggests, at least in the case of *specus*, that certain fragments which inhabit certain caves are starting to form cave-specific races. In pselaphids at least, this matter of raciation in cavernicoles has not been examined seriously. One of the difficulties is in obtaining enough material for study. At one time a cave may yield a score or more individuals, a few days or weeks later this cave may not produce a single individual, and a decade hence it may yield more of the population. This is not just a matter of poor collecting. The author feels that it emphasizes an insufficiently discussed aspect of cave ecology. The "cave" that we explore is, to a pselaphid, a vast domain. It may or may not contain an abundance of food, or have requisite shelter. It is subject frequently to vernal flooding. Under these several conditions, the "cave" may be a sudden expansion of the total current range of the population. In other words, the numerous cracks, solution passages and fractures which radiate from the "cave," often probably for great distances, or join "cave" to "cave," or "cave" to the earth's surface may house the bulk of the population. Such highways of dispersal would be in any direction, and need not be more than five millimeters diameter for ample exploitation.

If this is true then it explains partially the irregularity in obtaining cave pselaphids and further connotes a different type of hypogean population distribution. Micrometerological conditions might be even more constant in distant fractures than in the cave as such, and might contain a relatively higher proportion of food-animals.

The historical factor allows sufficient time for pselaphids to colonize cave systems, and in the area under examination there are many caves to penetrate. Such penetrations have taken place in the past, and are in process at the present time, if the information available has been interpreted correctly. In other words, if such a view is tenable we should expect a spectrum of adjustment, from highly modified cavernicoles without eyes and wings to chance occupancy by obviously epigean species.

Chance occupancy by trogloxenes probably occurs much more frequently than the number of attested examples would suggest. By the very nature of cave exploration, such recoveries would be few and the collection would be that of a single individual as a rule.

Three examples are known to the author: *Tmesiphorus costalis* LeConte, one specimen from Terrell Cave, Marshall County, Alabama; *Brachygluta illinoisensis* Brendel, Falling Water Cave in Tennessee; *Batrisodes* (*Pubimodes*) *denticollis* (Casey), Laurel Creek Cave, near Greenville, Monroe County, West Virginia. All three taxa are well-known, common, epigean species, the populations of which are broadly dispersed in the eastern United States. In each case, the cave collection was of a single individual.

At some point in the fortuitous evolution of a cavernicole a successful colonization must be attained. This must be by at least a pair, or a fertilized female. Its success should be attendant on an ability to meet initial competition, or be lodged in a recess where there is a temporary lack of competition for suitable space and/or food, yet having available such space and/or food. This combination of events is probably uncommon. For such an experiment, a taxon with high vagility is more apt to succeed.

An *a posteriori* choice for such a natural experiment would be *Batrisodes* (*Excavodes*) *globosus* (LeConte). This is one of the most widely dispersed, most abundant, autochthonous populations of the North American area. It is dispersed on the north from Quebec, Vermont and Massachusetts west to at least Vilas County, Wisconsin; south through Johnson County, Iowa, Douglas and Montgomery Counties, Kansas, and Washington County, Arkansas, to Texas and Natchitoches Parish, Louisiana, and hence eastward into central Florida. The species even has a trans-grassland outlier population in montane Colorado (Park, 1947). Over this range it is common in a variety of forest types, where it occupies a variety of forest floor habitat niches.

It has penetrated a variety of ant societies (Park 1932, 1935), including that of the prairie ant, *Formica cinerea neocinerea* Wheeler (Park, Auerbach and Wilson, 1953). It has become established in the society of the mound-builder, *Formica ulkei* Emery, as a facultative synoekete (Park, 1929, 1935).

Recently a colony of *globosus* has been discovered by Mr. Steeves in Turk's Cave, near Brooklyn, Conecuh County, Alabama. They are present in numbers under wood in the twilight zone. All evidence suggests that this is a resident, adjusted, breeding population. Struc-

turally they appear unmodified from the epigean *globosus* reservoir, *e.g.*, no change could be noted by the author in male secondary sex features, or vestiture and there was no significant reduction in the ocular facet number of the female sex — one of the first hallmarks of the emergent cavernicole.

Given sufficient time in this isolated spot, and given no chance for interbreeding with the epigean *globosus* population, this fragment may evolve, first as a new race, later as a new species. It is safe to assume that twentieth-century readers of this report will not be extant when and if these interesting events occur.

Turning from these suggested beginnings to an examination of the known cavernicolous fauna, we find at least three levels of structural modification.

First, there are three genera, *Batrisodes, Batriasymmodes,* and *Bythinopsis,* the cavernicolous species of which are thought of as having evolved from allied, epigean stocks within relatively recent geologic time, and to be evolving further and spreading geographically in the present period.

In *Batrisodes* and *Batriasymmodes* such species have a significantly reduced ocular facet number in the female sex. In *Bythinopsis* there is reduction in ocular facet number apparently in both sexes, but especially in males.

In other words, there has been enough anatomical change so that epigean populations can be differentiated from hypogean populations, but not enough modification for the latter to diverge generically.

Here belong the great majority of known cavernicoles in the American fauna.

Second, are elements that have diverged so much that they belong to genera or subgenera which do not have epigean representatives. They have lost the compound eyes entirely, and usually have lost the metathoracic wings. Their epigean allies are to be found in different genera or subgenera, within a given subtribe or tribe. Here belong *Machaerites* (subgenera *Speleochus* and *Subterrochus*) and *Arianops* (subgenus *Arispeleops*). Such elements tend to be even more uncommon, and to occupy a single cave, or at most several "caves" close enough to each other to be connected by subterranean fissures.

Finally, in a class by itself is the speleont *Speleobama vana* known from a single cave. It has lost eyes, wings, most foveae, has elongate appendages and bears a remarkable speleobamine ruff of setae. This ruff it shares with the only other speleobamine genus, the epigean *Prespelea* of the southern Appalachians, and to this extent could be placed in the preceding fourth category, where there are epigean allies at the tribal level. The difference is that the tribe Spoleobamini contains an admixture of characters, part of which belong to one great division of the subfamily Pselaphinae, and part of which to the other great division of this subfamily. Hence, its divergence is much greater structurally, apparently placing the tribe at the bottom of this large assemblage of pselaphines (Park 1951, 1953a, 1953b).

SUMMARY

There are thirty-three described species of cavernicolous Pselaphidae, divided among six genera, and three tribes.

This fauna is separated to species in a series of taxonomic keys, and assembled in a checklist which includes original citation and type locality for each species.

Described as new are *Arianops stygica, Batrisodes gemmoides, B. ferulifer, B. jocuvestus, B. clypeospecus, B. pannosus, B. tumoris, B. krekeleri, B. schneiderensis, Bythinopsis hubrichti, Machaerites croceus, M. eurous,* and *M. steevesi.*

A fungus, near the ascomycete genus *Stilbum,* is reported from *B. clypeospecus.*

Dimorphism has been found in the males of *Batrisodes pannosus.*

The subgenus *Batriasymmodes,* formerly in the genus *Batrisodes,* is raised to full generic status, with *monstrosus* (LeConte, 1850) as its genotype. New combinations resulting from the above action include: *B. troglodytes, B. spelaeus* and *B. quisnamus.*

Three synonyms are formed: *Batrisodes jeanneli* (Park, 1951), *B. reduncus* (Park, 1956) and *B. quisnamus* (Park, 1951) are synonyms of *Batriasymmodes quisnamus.*

In *Machaerites* the subgenus *Subterrochus* is described as new, with *ferus* (Park, 1951) as type of subgenus.

The probable role of small fissures from, or between caves is emphasized in the dispersal of cavernicolous pselaphids.

Seven major drainage systems have been utilized by this fauna. Of thirty-three taxa only two are found in more than one of these drainage systems. Twenty-two of these taxa, or about 67 percent, occupy one cave per taxon. Exceptions to these two generalizations are discussed, with special attention to two species of *Batriasymmodes.* Only one case is known in which more than one species in a given subgenus occupies the same cave.

As a background for a discussion of phylogenesis of cavernicolous pselaphids, their epigean allies are discussed briefly in terms of habitat niches occupied, response to illumination and moisture, feeding preferenda, and nocturnalism.

Cave penetration and evolution of cavernicoles are discussed in terms of (1) chance occupancy, and (2) a known instance of colonization of a given cave by the epigean *Batrisodes globosus.*

There appear to be three levels of structural modification. The first of these includes the genera *Batrisodes, Batriasymmodes,* and *Bythinopsis.* Each of these genera have both extant cavernicolous and epigean species. All of the cavernicolous populations are modified in that there is a reduction in the ocular facet number in one or both sexes.

The second group shows greater structural modification. Eyes are absent and metathoracic wings are usually absent. There is a tendency for elongation of appendages, paler integuments, and loss or size reduction in foveae. Here belong *Machaerites* (subgenera *Speleochus*

and *Subterrochus*) and *Arianops* (subgenus *Arispeleops*). These cavernicoles belong to genera or subgenera which do not have epigean representatives, that is, divergence is at the generic or subgeneric level.

Finally, the tribe Speleobamini has an admixture of basic structural features found in both branches of the subfamily Pselaphinae, that is, divergence is at the tribal group level. Here belongs *Speleobama vana* in which eyes, wings, vertexal, pronotal, and elytral foveae are absent, appendages are long and integument pale.

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The Occurrence of False Scorpions in Caves with Special Reference to Cavernicolous Adaptation and to Cave Species in the North American Fauna
(Arachnida - Chelonethida)

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Introduction

The false or pseudoscorpions are small, generally dorso-ventrally flattened arachnids belonging to the order Chelonethida. They hold especial interest from a speleological standpoint because a significant number are either obligate or facultative cave-dwelling forms. This is not at all surprising in light of the fact that these animals typically live in such habitats as under stones or bark, in crevices of all kinds, in the duff and debris of the forest floor, in the soil, and in other cryptic locations. The morphological and physiological characteristics fitting animals for these types of habitats need a minimum of adaptive change to allow exploitation of a cave environment.

Cavernicolous Modifications

As with many cavernicoles, one of the most common modifications is the loss of eyes. Although many pseudoscorpions are eyeless or provided merely with eyespots, most cave false scorpions are derived from groups which are normally four-eyed rather than blind. More characteristic than loss of eyes is a trend toward depletion of integumentary pigmentation. Cave pseudoscorpions also show a marked tendency to develop extremely slender and attenuated legs and palpi, especially in the highly troglobiont forms such as species of *Blothrus* Schiödte, *Pseudoblothrus* Beier, *Vachonium* Chamberlin, *Leucohya* Chamberlin, *Troglohya* Beier, and many others. All false scorpions depend more on the tactile than the visual sense.

False scorpions are provided typically with a battery of twelve highly specialized and sensitive tactile setae on the fingers of the chelae. Other tactile hairs frequently occur on the third and fourth pairs of legs as well as on the tip of the abdomen. Hence, they are already admirably adapted to a life in which tactation plays a primary functional role. In cave chelonethids there is a strong tendency to develop more elongate vestitural setae which also serve secondary tactile functions. The *main* development in cave species, however, is the attenuation of the appendages, particularly of the prehensile, chelate pedipalps enabling the animal to function more efficiently for purposes of defense as well as predation in an environment where the visual sense is of no value.

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An excellent example of pedipalpal attenuation is found in the genus *Neobisium* Chamberlin, which includes numerous cave as well as epigean species (Fig. 1C compared to Fig. 1D). A random selection of ten cave-dwelling and ten epigean species of this genus showed that the ratio of length to breadth of the palpal femur averaged 1.8 times as extreme in the cave as in the epigean members of the genus. Similarly, when comparing the ratio of length to breadth of the palpal chela and hand of the chela, the respective ratios were 2.0, 1.6, and 1.6 times as extreme in cave as in free-living species. In other words, the main segments of the palpi averaged from 1½ to 2 times as attenuated in cave as in epigean species of the genus. The chthonids, many of which are normally very slender in facies, also show this tendency although to a lesser degree (Fig. 1A in comparison to 1B). To illustrate, ten randomly selected epigean species of the genus *Tyrannochthonius* Chamberlin were selected and compared with the 11 known cave forms. The average ratio of length to breadth of the palpal femur, palpal chela, and hand of the chela was found to be 1.2 times as great in cave species as in epigean forms, while the ratio for the palpal tibia was 1.1 times as extreme.

The development of giantism (Fig. 1) among many cavernicolous pseudoscorpions is a very characteristic and indeed typical modification. The trait has apparently arisen independently in most, if not all, true troglobiont chelonethids. Using the length of the palpal

Fig. 1.—Comparison of pedipalps of epigean and troglobiont false scorpions. A and B: Chthoniidae. A. Dorsal view, palp of an epigean *Tyrannochthonius* from Florida. Compare with B, the palp (ventral aspect) of a troglobiont species of the same genus from Alabama. Same scale of magnification. C, D: Neobisiidae. C. Ventral view, left palp of a typical epigean species, *Neobisium* (N.) *sylvaticum* (L. Koch). Compare with D, the right palp (dorsal aspect) of a typical troglobiont, N. (*Blothrus*) *abeilli* (Simon). Drawn to same scale.

femur, the palpal hand and fingers of the chela as indices of size, this phenomenon is easily demonstrated. *Neobisium* with its large number of both epigean and cave forms was selected for study. A comparison of nine epigean and nine cave species of this genus, selected at random, showed that the lengths of femur, hand, and fingers averaged 2.5, 2.3, and 2.1 times as long in the troglobiont (subgenus *Blothrus*) species as in the epigean (subgenus *Neobisium*) forms. Giantism reaches its most extreme expression in two species of this genus, *N.* (*B.*) *maderi* Beier and *N.* (*B.*) *biocovense* Müller, in which the lengths of palpal femora are 4.0 and 4.5 mm, respectively. In the false scorpion world, where total body length often may not exceed 1-2 mm, this is truly immense! A glance at other groups of false scorpions shows that this tendency is not limited to the neobisioids. For example, length of palpal femur and chela of seven randomly selected cavernicolous species of *Tyrannochthonius* averaged 1.7 and 1.8 times as long as the average in nine epigean members of the same genus. The adaptive value of this increased size remains obscure but may be related to the size of available prey in a cavernicolous environment.

RELATIONSHIP OF CAVE SPECIES TO TAXONOMIC CATEGORIES

A survey reveals that of 1,857 species and subspecies of false scorpions thus far enumerated for the world, 293 are cavernicolous to a greater or lesser extent. Thus, 16 per cent of all known chelonethids either may or must live in caves. This is indeed a high percentage of representation to be found for an entire order. However, further study (summarized in Table I) shows some even more interesting facts. Of the 293 cavernicolous forms, 268 are members of the two superfamilies Chthonioidea and Neobisioidea, these two superfamilies contributing 92 per cent of all cave species found in the order while comprising only 37 per cent of the total number of species. Furthermore, 89 per cent of the genera which are known only from cave forms belong to these two groups. Thirty-two per cent of all chthonioids are cavernicoles to some degree, while 44 per cent of all neobisioids fall in the same category. Considering these superfamilies together, 39 per cent of all species are cavernicolous. In none of the other four superfamilies does the percentage of cavernicoles exceed 3 per cent.

The American fauna north of Panama comprises approximately 314 species (including presently recognized but as yet unnamed cave forms). This is about one-sixth of the world total. Of the American species, 43, or 14 per cent are known from caves — a value very closely comparable to the 16 per cent incidence in the world fauna. Also, as for the world fauna, the great majority of cave forms belong to the superfamilies Chthonioidea and Neobisioidea where the percentage of included cave species is 46 and 27, respectively (35 per cent considering both groups as a unit).

Why the preponderance of cavernicoles in the two superfamilies

Chthonioidea and Neobisioidea? The answer appears to lie in the ecological habits of the members of the two groups. Basically, they are leaf-mold and soil-inhabiting forms. Although they are normally four-eyed, there is a strong tendency toward the loss of the posterior eyes even in epigean forms. Most species are typically retiring and rather sluggish inhabitants of damp duff and humus, lying in wait for their prey, rather than actively pursuing it. The overwhelming majority of the true troglobiont forms are derivatives, then, of mois-

Table I—Incidence of cave species[1] in the order Chelonethida (manuscript genera and species are excluded)

Superfamily or Family	False Scorpion Genera[2] World total	No. with cave species	Per cent with cave species	Total No. of species	Cave species No.	Cave species Per cent
CHTHONIOIDEA						
Tridenchthoniidae	17	1	6	50	1	2
Chthoniidae	31	16	52	225	88	39
Total	48	17	35	275	89	32
NEOBISIOIDEA						
Neobisiidae	15	8	53	356	162	46
Ideoroncidae	10	2	20	22	3	14
Syarinidae	8	5	62	20	9	45
Hyidae	4	2	50	5	2	40
Vachoniidae	3	2	67	5	3	60
Total	40	19	48	408	179	44
GARYPOIDEA						
Menthidae	1	0	0	4	0	0
Olpiidae	34	0	0	168	0	0
Garypidae	13	1	8	94	2	2
Total	48	1	2	266	2	0.8
FEAEOLLOIDEA						
Pseudogarypidae	3	0	0	8	0	0
Feaellidae	1	0	0	8	0	0
Total	4	0	0	16	0	0
CHEIRIDIOIDEA						
Cheiridiidae	8	0	0	31	0	0
Sternophoridae	2	0	0	9	0	0
Total	10	0	0	40	0	0
CHELIFEROIDEA						
Atemnidae	18	1	6	151	1	0.7
Myrmochernetidae	1	0	0	1	0	0
Chernetidae	86	11	13	393	18	5
Cheliferidae	77	4	5	307	4	1
Total	182	16	9	852	23	3
TOTAL	332	53	16.0	1857	293	15.8

[1] For purposes of this tabulation no distinction is made between species and subspecies. Data from published records to 1958.

[2] Includes "artificial" cave subgenera of *Allochthonius, Chthonius, Neobisium,* and *Roncus.*

ture loving, soil- and humus-inhabiting species — in other words, those that are almost "subterranean" in habit to begin with.

Practically no cavernicoles are found in the Garypoidea and none at all in the Feaelloidea and Cheiridioidea. The garypoid cavernicoles (two species) of the genus *Larca* Chamberlin are true troglobionts from Spanish caves. In the large superfamily Cheliferoidea, which includes nearly half of the described false scorpion species, a modest number of cavernicoles occur (about 3 per cent of the world total). These belong primarily to the single family Chernetidae, all species of which are blind. Many species of this family are recorded from the nests of ants and other social insects, bird, rodent or other small animal nests, and more important, from our standpoint, in association with bats. It is easily seen how such pseudoscorpions living in intimate commensal relationships with such an animal as a bat could be carried into caves and from cave to cave with the "host." Most known (as well as presently undescribed) cavernicolous cheliferoids, principally chernetids, are found exclusively in bat caves. It is highly probable, therefore, that the basic association is between the pseudoscorpion and the bat rather than between the pseudoscorpion and the cave. Hence, we regard these forms as primarily "chiropterophiles" and only secondarily as troglophiles. Thus, morphological specializations normally arising from cave habitation are rare or completely lacking. A few other species in this superfamily reported from caves may be considered to be trogloxene in habit. That is, they are found only in the twilight zone of caves and in many instances are merely epigean forms that have gained fortuitous entrance.

Faunistic Derivation of Cave Species

In general, the chelonethid cave fauna is derived from the epigean forms existing in the same general geographical area, a point already made by Beier (1940) in his review of the phylogeny of European cave-dwelling pseudoscorpions of the families Chthoniidae and Neobisiidae. The chelonethid fauna of Europe, both epigean and cave, is much better known than that of any other part of the world. Thus, Beier was able to trace probable lines of evolution within the common European genera. These genera are not, however, the same as those contributing to the North American cave fauna, but, as one would expect, most closely related to epigean European forms. In Europe, the genera *Neobisium* and *Roncus* L. Koch in the broad sense, provide the majority of troglobionts. The number is large, and within each genus a polyphyletic subgenus (*Blothrus* and *Parablothrus* Beier, respectively) has been recognized for the reception of most of the cavernicoles.

The only exceptions to the rule that cave forms are derived from the existing epigean fauna of the same area, are a few species which can best be understood as relict forms — or shielded remnants of an earlier fauna. For example, *Troglochthonius* Beier is a monotypic, troglobiont genus from the Balkans. It is considered to be an offshoot

of *Tyrannochthonius* which does not now live in that geographical area. The same is likely true of other relict genera of Europe such as *Hadoblothrus* Beier, *Pseudoblothrus,* and *Troglobisium* Beier of the family Syarinidae, not otherwise represented in Europe.

Investigation of the North American chelonethid cave fauna is still in its infancy. Practically all collections of cave false scorpions made in the United States have come from limestone caves east of the Mississippi River, despite extensive caverns in Texas, New Mexico, Arizona, Utah, Oregon and other parts of the West and Southwest. The caves thus far explored in Texas have been bat caves, and as would be expected only chernetid chiropterophile species have been found. Only from the relatively well-investigated caves of eastern United States and southern Mexico have true troglobiont forms been collected.

In North America, in contrast to Europe, there are no cave species of the genus *Chthonius* C. L. Koch, their place being taken by representatives of other genera such as *Kleptochthonius* Chamberlin, *Tyrannochthonius,* or *Chamberlinochthonius* Vachon. In the Neobisiidae, cavernicolous species of *Neobisium* and *Roncus* are numerous in European caves but rare in North America. Troglobiont species of the holarctic genus *Microcreagris* Balzan are now known from both European (Portugal) and the United States caves. Two new species of the syarinid genus *Chitrella* Chamberlin from eastern caves have recently been described (Malcolm and Chamberlin, 1960). The most highly specialized of all North American cave forms, however, are true troglobionts from Mexico belonging to the families Hyidae and Vachoniidae. Since epigean species of these two small families are not known from America, they may represent true relict forms.

SYNOPTIC REVIEW OF THE NORTH AMERICAN CAVE GENERA

Superfamily Chthonioidea Chamberlin

Family Tridenchthoniidae Balzan

The small family Tridenchthoniidae is predominantly tropicopolitan in distribution and is rather poorly known at present. *Tridenchthonius juxtlahuaca* Chamberlin and Chamberlin is the only species thus far described from a cave (Cueva de Juxtlahuaca, Colotlipa, Mexico). It was presumably collected from bat guano. It is closely related to an epigean species described from the same general area (*T. mexicanus* Chamberlin and Chamberlin) and in any case is at most a troglophile if not merely a trogloxene.

Family Chthoniidae Hansen

The Chthoniidae is a large family of world-wide distribution. A high percentage of the known troglophilic and troglobiont false scorpions belong to this family.

In North America the chthoniid cave species are represented by the genera *Kleptochthonius, Chamberlinochthonius, Tyrannochthonius, Apochthonius* Chamberlin (?) and a presently undescribed and rather unique monotypic genus. The cave representatives of all these genera except *Apochthonius* are mostly true troglobionts. The species representing these genera are known from various of the extensive limestone caverns which are common throughout the Appalachian region including Indiana, Kentucky, Tennessee, West Virginia and Alabama.

It is of interest to note that the earliest records of cavernicolous false scorpions from America included representatives of this family. Thus the three species discussed by Packard (1886) were: *Chthonius packardii* Hagen (= *Kleptochthonius packardii* (Hagen)) from Wyandotte Cave in Indiana; *Chthonius coecus* Packard (= *Apochthonius* (?) *coecus* (Packard)) from Weyer's Cave, Virginia and *Obisium cavicola* Packard (= *Chitrella cavicola* (Packard) *teste* Wm. B. Muchmore, (1959)) from New Market Cave, Virginia. It seems certain that *Chthonius packardi* as described by Hagen and redescribed and discussed by Packard is a composite of several species and the true identity of all specimens recorded under this name other than those of the type collection from Wyandotte Cave are suspect.

Genus *Apochthonius* Chamberlin

The genus *Apochthonius,* represented by five described species, is widespread throughout much of the United States. Individuals are common in forest litter, moss and similar environments. It seems probable that the species *Chthonius coecus* Packard (1884, Amer. Naturalist, 18:203) properly pertains to this genus, or, less probably, to *Mundochthonius* Chamberlin — a question that can only be settled by restudy of the type or of topotypical material. It is certain that it does not belong to either *Chthonius* or *Kleptochthonius.* The species is not of troglobiont facies and may be either a trogloxene or, at most, a troglophile.

Undescribed New Genus

Specimens of an unusual, undescribed troglobiont species are at hand which represent a new genus having no close affinities to any other American genus. They were collected in an Alabama Cave and may represent a true relict form.

Genus *Kleptochthonius* Chamberlin

The genus *Kleptochthonius* comprises three described species (one a cave dweller) from the eastern part of the United States, particularly the southeastern states. One of these species, *K. packardi*

(Hagen) described from Wyandotte Cave in Indiana, has already been discussed. In addition to these described forms, Chamberlin and Malcolm have in manuscript, descriptions of 7 new species belonging to this genus — 5 troglobionts from Tennessee and Virginia and 2 epigean forms from Oregon. One representative of the epigean species *K. multispinosus* Hoff is currently at hand from an Alabama cave. Thus of 10 described and manuscript species of *Kleptochthonius* known to us 60 per cent are exclusively from cave habitats.

Genus *Chamberlinochthonius* Vachon

The genus *Chamberlinochthonius* at the present time contains but a single species, *C. henroti* Vachon, a true troglobiont from MacClung's Cave in West Virginia. *Kleptochthonius* and *Chamberlinochthonius* are very similar in most respects and future study may require a redefinition of the two genera with *Chamberlinochthonius* possibly falling as a synonym or being relegated to subgeneric rank.

Genus *Tyrannochthonius* Chamberlin

The genus *Tyrannochthonius* is widely distributed but basically tropicopolitan in distribution. In addition, certain subtropical epigean forms, as yet undescribed, occur in the southern United States (Florida and Arkansas).

In extensive cave collections from Alabama we have found 11 typical troglobiont species and subspecies belonging to this genus. Including certain undescribed, free-living species *Tyrannochthonius* in its broadest sense is now known to include a total of 61 species and subspecies of which one is a trogloxene from a Mexican cave while 11 are true troglobionts from various caves in Alabama. Thus, roughly 20 per cent of the known species in this genus occur in caves.

Superfamily Neobisioidea Chamberlin
Family Neobisiidae Chamberlin

The genus *Neobisium* which is so abundant both in numbers and species in Europe is represented in North America by a single variable species restricted to the eastern seaboard of the United States. It has not been found in caves — not even in the twilight zones, although such occurrences should be anticipated.

Genus ***Parobisium*** Chamberlin, new genus

Generic type: *Neobisium* (*Parobisium*) *magnum* Chamberlin.

The genus *Parobisium*, originally considered a subgenus of *Neobisium* (Chamberlin 1930, Ann. Mag. Nat. Hist. London ser. 10: 5:17), is here elevated to full generic rank. It will undoubtedly be found to be a large genus with many species in the Orient (China, Japan) and in northwestern North America. Cave species have

already been described from Japanese caves by Morikawa (1957) although none seem to be more than troglophilic in character. One described epigean species is presently known from Oregon. In addition we have at hand a second unnamed species collected from one of the numerous lava caves near Redmond, Oregon. The species is blind and attenuate but of nearly normal pigmentation — possibly only a trogloxene.

Genus *Microcreagris* Balzan

The genus *Microcreagris* is an extremely wide ranging (holarctic) genus comprising a very common element of the forest floor fauna wherever it occurs. Its species normally possess 4 large eyes. Although generally favoring a moist to damp environment, true desert forms are known. In most respects it seems to fill the same ecological niche held by *Neobisium*. Hence it would appear to be a natural source of cave inhabitants. Surprisingly, the only true troglobiont thus far described is *M. cavernicola* Vachon from Portugal. However, we have at hand three manuscript troglobiont species from caves in Tennessee and Alabama, indicating the possibility that many more await description.

The only North American species of *Microcreagris* thus far recorded from a cave is *M. phyllisae* Chamberlin, an epigean form from Eaton's Cave (Los Angeles County) in California. Including manuscript forms the apparent incidence of cave species in *Microcreagris* is at least 7 per cent.

Family Syarinidae Chamberlin

The small family Syarinidae is at present inadequately known but is of outstanding speleological interest in being represented by three highly specialized, troglobiont relict genera of Europe. Two American genera of the family are presently known to include cave species.

Genus *Chitrella* Chamberlin

The genus *Chitrella* is currently composed of six species which are nearctic in distribution. The typical habitat is in leaf mold, soil, and under stones. Three of the 6 species are new (Malcolm and Chamberlin, 1960). Of these, two are from caves in Tennessee and West Virginia. *Obisium cavicola* Packard, collected from New Market Cave in Virginia also belongs to this genus (*teste* Muchmore 1959). Therefore, of the six species in the genus, three are exclusively cavernicolous.

Genus *Pachychitra* Chamberlin

The genus *Pachychitra* is presently known from three species from the Caribbean area, one of which (*P. maya* Chamberlin) was described from near the mouth of a cave in Yucatan where its occurrence may well have been fortuitous.

Family Vachoniidae Chamberlin

The rare family Vachoniidae is known from three genera — one a genus of free-living species occurring in South Africa and two cave genera (including three troglobiont species) from Mexico. These are *Vachonium boneti* Chamberlin (Yucatan, Cueva de Sabaca); *Vachonium maya* Chamberlin (Yucatan, Cueva de Balaam Canche, Chichen Itza); and *Paravachonium bolivari* Beier (Tamaulipas, Cueva de Quintero).

Family Hyidae Chamberlin

The family Hyidae is known from a mere handful of species grouped in four genera. Two of these are represented by epigean species only (*Hya* Chamberlin (from the Philippine Islands, Java and Sumatra) and *Parahya* Beier (from Micronesia)). The other two genera are monotypic and include the two most extreme troglobiont species yet found in the North American fauna (*Leucohya heteropoda* Chamberlin (Neuva Leon, Gruta del Palmito) and *Troglohya carranzai* Beier (Northern Oaxaca, Cueva de Monteflor)).

Superfamily Cheliferoidea Chamberlin
Family Chernetidae Chamberlin

The large family Chernetidae is of cosmopolitan distribution. No true troglobiont species are known although a fair number of species have been recorded from caves, primarily bat caves, and usually on or associated with guano deposits. All species are eyeless so that blindness *per se* has no significance in this family as far as cave adaptation is concerned. None of the species known to us is significantly modified in a troglobiont direction and, except for a number of trogloxene forms which have wandered into the mouths and near the entrances of caves, most known species may be considered primarily chiropterophile and only secondarily troglophile in habit.

Published records of chernetids from American caves are extremely few. Two species (*Lustrochernes minor* Chamberlin and *Parazaona cavicola* Chamberlin) have been recorded from Yucatan Caves. One species (*Tejachernes stercoreus* (Turk)) was taken from bat guano in Bracken Cave, Texas, while *Pseudozaona mirabilis* (Banks) was described from Indian Cave, Barren County, Virginia.

In addition to the published records, numerous specimens from various caves in Alabama, Texas, Mexico and a few other North American localities are at hand—most of these appear to belong to the genera *Pseudozaona* Beier, *Hesperochernes* Chamberlin and *Dinocheirus* Chamberlin.

RECAPITULATION

In summary we may say that the 16 per cent of the species of the order Chelonethida which are found in caves come predominantly from two superfamilies, the *Chthonioidea* and the *Neobisioidea*. This can be explained on the grounds that these two groups basically consist

of moisture-loving, soil and humus-inhabiting forms that easily adapt to cave environments. The question arises, however, as to why the troglobiont habit evolved repeatedly in certain genera, while in closely related genera, living in much the same type of habitat, troglobioncy has never appeared. It is a question that piques the imagination and interest, but at present no answer is available.

In common with other cavernicolous animals, false scorpions which have adapted themselves to this environment often lose their eyes and body pigment. In addition, attenuation of appendanges and giantism are frequent modifications.

The distribution of troglobioncy in the chelonethids, both geographic and phylogenetic, can best be explained as an outcome of the origin of cave forms from the epigean species of the area surrounding the cave. Those cave species which are geographically isolated from related epigean forms can logically be explained as relict species of earlier faunas.

The North American cave fauna is composed primarily of the chthoniid genera *Tyrannochthonius, Kleptochthonius* and *Chamberlinochthonius* instead of *Chthonius* as in European cave fauna. In place of *Neobisium* and *Roncus,* so dominant among cave false scorpions in Europe, we find the neobisiid genera *Microcreagris* and *Parobisium* and the syarinid genus *Chitrella*. In addition, Mexican caves contain such unique and possibly relict genera as *Leucohya* and *Troglohya* of the Hyidae and *Vachonium* and *Paravachonium* of the Vachoniidae. In bat caves we find representatives of *Parazaona, Pseudozaona, Tejachernes* and other chernetids which, in contrast to the neobisioid and chthonioid forms, are to be considered primarily chiropterophile and only secondarily troglophile in nature.

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Speciation in North American Cave Millipeds

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Millipeds rank probably third among terrestrial arthropods — after the insects and arachnids — as to the number of cave-adapted forms. Some groups of them, notably the suborder Chordeumidea, have produced many cavernicoles; other groups have produced none, possibly because of some intrinsic factor and not lack of proximity to caves.

Typical millipeds spend their lives in humus, rarely moving from it except at night. The humus supplies all of their needs: food and protection from desiccation, light, and extreme temperatures. The food is usually decaying vegetable matter, sometimes fungi, decaying animal matter, or animal excrement. Because most millipeds lose water readily through the exoskeleton, they do not wander far from a continuously moist substratum. Caves would seem to offer a more certain source of uninterrupted humidity than most epigean habitats.

Millipeds usually have been regarded as a very uniform group with regard to water relations, but actually a wide range exists in their humidity reactions, a range stated by Perttunen (1953) to be as wide as that among insects. Large, heavy-bodied forms tend to be euryhygric and smaller forms stenohygric, but within each size range a great variety exists in the humidity reactions. Measured evidence of this is scarce, for the study of the class Diplopoda is still in the descriptive stage.

Millipeds collected in caves fall into three ecological groups, viz., epigean forms that have entered accidentally, facultative cavernicoles, and obligate cavernicoles. It is often impossible to determine to which ecological group a particular form belongs on the basis of morphological characters alone, for millipeds are a conservative group, and cave-induced modifications are seldom spectacular. Bizarre cave-adapted forms are rare.

The accidental cave entrants usually have pigmented, heavy exoskeletons and include both small-bodied and large-bodied forms. They wander into caves, fall in, are washed in by flood waters, are driven in by drought, or are carried in by other animals. And since caves have been studied so much more thoroughly than most epigean areas, some epigean forms are known only from cave collections.

The facultative cavernicoles, or troglophiles, are epigean forms with great moisture requirements that usually live in deep humus, but they are also tolerant of cave conditions and sometimes reproduce there. Some troglophiles have the somatic modifications that are associated with obligate cave life: reduction of body pigment, elongation of legs and antennae, a thinner exoskeleton, and loss of some or all of the ocelli. Others show these modifications only to a slight degree or

not at all. *Cambala minor* is a common troglophile in the eastern United States, and there are three conotylids in the upper Mississippi Valley that are troglophiles. Possibly some of the pseudotremias are troglophiles also.

The most conspicuous modifications of obligate cavernicoles, or troglobites, is the loss of body pigment, leaving them either white or some pale shade of brown or yellow; the latter colors often darken upon preservation. The thickness of the exoskeleton seems to vary with the group, as it does in epigean forms. In some forms the exoskeleton is so thin that it wrinkles in dry air, while in others it is almost as thick as in related epigean forms. The legs and antennae are thinner and longer than in closely related epigean forms, but rarely to a marked degree. The sensory setae are usually elongated in relation to the lengthening of the legs and antennae, but they seem to be less numerous than in some epigean forms. The body tends to be slightly larger than in the closest epigean relatives; gigantism is rare. The body length ranges from about 5 mm to 60 mm; most species are between 8 and 30 mm long.

In a few species, the cave modifications are great enough to produce a striking appearance. *Speodesmus bicornourus,* a Texas troglobite, has the legs and antennae so elongated and the body so narrow and loose-jointed that it resembles a centiped more than a milliped. *Speostriaria shastae,* from a California cave, is a giant, about twice the length of any other striariid and the only one with elongated legs and antennae. It is of special interest because it is the only troglobitic milliped that is known from both Pleistocene and Recent specimens. The ocelli have persisted and are as numerous and almost as deeply pigmented as in epigean striariids, but there is no body pigment.

The study of North American cave millipeds began with E. D. Cope, who is remembered chiefly for his work in vertebrate paleontology. He described *Pseudotremia cavernarum* and proposed the genera *Pseudotremia* in 1869 and *Scoterpes*[1] in 1872; these are the largest and most complex milliped genera in our cave fauna. A. S. Packard, Jr. described a polydesmid from a desert cave in Utah (1877) and two chordeumids from Kentucky caves (1871, 1883). In his "Cave Fauna of North America" (1886), he included figures of the brains of *Pseudotremia* sp. and *Scoterpes copei,* which he sectioned and examined for the presence of optic nerves and optic ganglia. John A. Ryder (1880) added the third great eastern cave genus, *Zygonopus,* for Virginia and West Virginia trichopetalids. During Charles H. Bollman's brief, brilliant career, he described (1887) one cavernicole, *Scytonotus cavernarum,* from Mayfield's Cave, Monroe Co., Indiana; unfortunately, this milliped has not been identified in

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1 Although *Scoterpes* was first mentioned in a paper on the fauna of Wyandotte Cave, in Indiana, the genus does not occur that far north; it was proposed for *Pseudotremia copei* Packard from Mammoth Cave, Kentucky, which is at the northern limit of the range of the genus. A paper on *Scoterpes* is in preparation.

later collections. Jerome McNeill (1887) described *Trichopetalum bollmani,* now in the genus *Conotyla* and known from several Indiana caves.

At the end of the nineteenth century the literature species of North American troglobites consisted of two polydesmids and five chordeumids. The latter were brought together, with excellent descriptions and figures of some, in Cook and Collins' "Craspedosomatidae of North America" (1895). These authors added no more cave species, but they proposed the genus *Conotyla,* which includes both epigean and troglobitic forms.

The collections made by Mr. Kenneth Dearolf and Mr. Leslie Hubricht from caves in the eastern United States provided the material for the important 1939 and 1943 papers of H. F. Loomis and opened a new phase in the taxonomy of cave millipeds. In these and later papers (1944, 1953), Loomis added three genera and 17 species. R. V. Chamberlin has worked on two important cave collections from Mexico (1938, 1942), and has added two genera and several species and a subspecies from caves in Georgia and the western states (1943, 1952, 1953b). Several of the other species that he described (1953a, 1953b) were collected in caves, but they probably are not troglobites. Richard L. Hoffman (1950, 1956) has added two genera, several species, and a subspecies from the eastern states. Nell B. Causey (1958, 1959, 1960) has been fortunate in having the large collections of Dr. Thomas C. Barr, Jr., the Cave Research Associates, and several members of the National Speleological Society for study. She has added two genera and several species and has others in press.

Fossil specimens of two species from caves in northern California were described by Fordyce Grinnell, Jr. (1908). They should be restudied.

In the "Checklist of the Millipeds of North America" (Chamberlin and Hoffman, 1958), 29 species and subspecies, or approximately 4 percent of all species listed are troglobites. Since the publication of the "Checklist," several other troglobites have been described, and many others have been collected. The total number — both described and undescribed — is more than 90 species and subspecies, representing 21 genera and 4 orders. The final revised percentage of troglobitic species probably will be greater than 4 percent because of the high endemism in the genus *Pseudotremia.* Of the estimated number of species and subspecies, four orders are represented as follows: Chordeumida, 80 percent; Polydesmida, 15 percent; Cambalida, 3 percent; Julida, 2 percent. Of the epigean species and subspecies listed in the "Checklist," these same four orders are represented as follows: Chordeumida, 16 percent; Polydesmida, 40 percent; Cambalida, 4 percent; Julida, 20 percent. The remaining 20 percent of the epigean species are divided among six orders.

Troglobitic millipeds occur in wet caves as far back as there is any organic matter. There is one report of a collection of *Scoterpes copei* three or four miles from the entrance of Mammoth Cave (Cope, 1871). They feed on anything organic, as wood, guano, rat pellets,

tree roots, or paper. Many caves have no millipeds. Dr. T. C. Barr, Jr., who visited more than 700 caves in the Tennessee part of the Cumberland Plateau from 1954 through 1957, found millipeds in about 10 percent of them. Of the Tennessee caves with millipeds, about 90 percent have only one species, and only one cave, Cumberland Caverns, Warren County, has as many as four species. This is in an area where epigean conditions are very favorable for millipeds.

Isolated caves tend to be occupied either by monotypic genera or by relics of widely distributed genera that also have epigean species. In areas where caves are numerous and close together, endemism is great, but sometimes no greater than among epigean groups in which explosive evolution has occurred. Endemism is greatest in the caves of the Nashville Basin, where caves within sight of each other may each have a population of *Pseudotremia* different from that of any other cave. This is the most successful cave genus in number of taxa, number of individuals, number of caves occupied, and extent of the cave area occupied. The rare epigean members of this genus occupy a small range that is within the range of the troglobitic members.

Nothing is known about method of distribution of troglobitic millipeds. The pattern of distribution of one species may follow an existing stream course, and in another species in the same genus, it may cut directly across both stream courses and mountains. The map showing the distribution of the four species of the completely troglobitic genus *Zygonopus* (Causey, 1960a, Fig. 1) suggests that some factor other than existing streams has determined the distribution. The most unusual pattern of distribution is exhibited by the completely troglobitic genus *Scoterpes*, of which 27 taxa are now known. One group of them occupies caves in the Nashville Basin, and another and more primitive group occurs in caves on the margin of the range

Fig. 1. The distribution of troglobitic millipeds in the United States.

in Missouri, Kentucky, the Great Basin of eastern Tennessee, and northern Alabama and Georgia.

The distribution of troglobitic millipeds in the United States, as shown in Figure 1, is incomplete, for many caves still have not been explored for them. The states in which they occur are listed here. For the states west of the Mississippi River, all known species, both described and undescribed, are mentioned, but for the eastern states where there is so much endemism, the names of many species have been omitted. Additional names of species in the eastern states can be found in the "Checklist" (Chamberlin and Hoffman, 1958) and in other references at the end of this paper.

Oregon.—Troglobites have been reported, but they have not been seen by a taxonomist.

California.—*Speostriaria shastae* (Causey), Samwel Cave, Shasta Co.; *Striaria eldora* Chamberlin, Eldorado Co. and Calaveras Co. (this may be a troglophile); conotylids from Shasta Co., Lassen Co., and Siskiyou Co.; polydesmids from Mendocino Co., Napa Co., and Santa Cruz Co. Several species (Chamberlin 1953a, 1953b) that have been described from collections from California caves probably are epigean.

Nevada.—*Tidesmus hubbsi* Chamberlin, a cave deep in Cave Valley, Lincoln Co.; a conotylid from White Pine Co.

Utah.—*Brachydesmus cavicola* (Packard), Clinton's Cave, Tooele Co.

New Mexico.—*Speorthus tuganbius* Chamberlin and another small polydesmid, Carlsbad Caverns, Eddy Co.

Texas.—*Speodesmus echinourus* Loomis, several caves in Hays Co., Kendall Co., and Kerr Co.; *Speodesmus bicornourus* Causey, Beck's Ranch Cave, Williamson Co.; *Eclomus specobius* Chamberlin, Wyatt Cave, Sutton Co.; *Cambala caeca* Loomis, caves in Sutton Co.; *Cambala captiosa* Causey, caves in Williamson Co. and Bexar Co.; *Cambala* sp., Val Verde Co.; a small, eyeless cambalid from Wheeler Co. It is doubtful that all three of the cambalids described from the southwestern counties are full species.

Missouri.—*Tingupa pallida* Loomis and *Tingupa* sp. from the following counties: Benton, Boone, Camden, Crawford, Franklin, Maries, Marion, Miller, Jefferson, Phelps, Pulaski, Ripley, Texas, and Wayne; *Scoterpes dendropus* Loomis, Stone Co. and Barry Co., also reported from Jefferson Co. and Franklin Co.; *Zosteractis interminata* Loomis, St. Louis Co., Ste. Genevieve Co.; *Conotyla specus* Loomis is a troglophile.

Illinois.—*Tingupa pallida* Loomis, reported from western counties.

Indiana.—*Conotyla bollmani* (McNeil) from the following counties: Lawrence, Orange, Monroe, and Washington; *Pseudotremia indianae* Chamberlin and Hoffman, Crawford Co.; *Scytonotus cavernarum* Bollman, Mayfield's Cave, Monroe Co.

Ohio.—*Pseudotremia* sp., Adams Co.

Pennsylvania.—*Conotyla vaga* Loomis from the following counties: Berks, Dauphin, Mifflin, and Blair.

Maryland.—*Conotyla vaga* Loomis, Washington Co.

Virginia.—*Pseudotremia cavernarum* Cope, Erhart's Cave, Montgomery Co.; *Pseudotremia* spp., western counties; *Zygonopus whitei* Ryder, Page Co. and Shenandoah Co.; two other species of *Zygonopus*, western counties.

West Virginia.—*Pseudotremia* spp., eastern and southern counties; *Dearolfia lusciosa* Loomis, Pendleton Co.; *Zygonopus whitei* Ryder, Pendleton Co.; three other species of *Zygonopus*, eastern counties.

Kentucky.—*Pseudotremia* spp., eastern and middle counties; one species of *Zygonopus,* Estill Co.; *Scoterpes copei copei* (Packard) from the following counties; Adair, Barren, Edmondson, and Hart; *Scoterpes* spp., southern counties; *Antriadesmus fragilis* Loomis, Edmondson Co., is a troglophile.

Tennessee.—*Pseudotremia* spp., eastern and middle counties; *Scoterpes* spp., eastern and middle counties; *Tetracion tennesseensis* Causey, Warren Co., White Co., and Grundy Co.; *Tetracion jonesi antraeum* Hoffman, Franklin Co.; *Antriadesmus mollis* Causey, Warren Co.; *Antriadesmus debilis* Causey, Wayne Co.; two other small polydesmids, Jackson Co. and Morgan Co.; *Ameractis satis* Causey, from the following counties: Cumberland, Hamilton, Overton, Putnam, and White.

Georgia.—*Pseudotremia* spp., northwestern counties; *Scoterpes* spp., northwestern counties.

Alabama.—*Pseudotremia* spp., northeastern counties; *Scoterpes* spp., northeastern counties: *Tetracion jonesi jonesi* Hoffman, Marshall Co.; *Tetracion jonesi antraeum* Hoffman, Jackson Co. and Madison Co.; *Troglocambala loomisi* Hoffman, Jackson Co. and Madison Co.; *Troglocambala loomisi* Hoffman, Turk's Cave, Conecuh Co.; a small polydesmid, northeastern counties.

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Checklist of Macroscopic Troglobitic Organisms of the United States

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The first attempt at a systematic classification of cavernicolous organisms was made by Schidote (1851). He grouped cavernicoles into *Skyyge-Dyr* (shade animals), *Tusworke-Dyr* (twilight animals), *Hule-Dyr* (cave animals) and *Drypsteenhule-Dyr* (stalactite animals). In the first class were placed those organisms having a preference for a cool, moist habitat and which were occasionally found at cave entrances. The second class consisted of organisms that periodically penetrated into the dark recesses of the cave. The third class was composed of organisms that lived their whole life in total darkness; the terrestrial forms were blind, while the aquatic forms had organs of sight. Finally, in the fourth class were blind, wingless, nonpigmented forms.

Schiner (1854) modified this classification and first proposed the three categories which are the basis for cavernicolous classification today. The first, trogloxenes, includes all organisms which may be found occasionally in caves. They do not complete their life cycles in total darkness. The trogloxenes are predominantly an epigean fauna although some hypogean arthropods are included in this group. In the second category are the troglophiles, organisms that spend part or most of their life cycle in caves. Some of these are adapted for a hypogean existence and thus readily survive in the cave habitat. A majority of troglophiles are facultative cavernicoles while all the members of the third group, the troglobites, are obligative cavernicoles. These are blind or have nonfunctional optic organs, manifest little pigmentation and have developed highly sensitive tactile organs.

In 1896, Hamann, utilizing Schiner's categories, classified all the known European cavernicoles and listed 382 troglobitic species, although many were subsequently regrouped as troglophiles or trogloxenes. His list included one vertebrate (*Proteus anguinus*), 16 gastropods, 229 insects (including 196 Coleoptera), 14 myriapods, 5 chilopods, 83 arachnids, 10 crustaceans and 24 other species in other orders. Although numerous papers on cavernicoles were published during the next thirty-five years by such eminent investigators as Chappuis, Cope, Jeannel, Martel, Packard, Racovitza and Spandl, it was not until the appearance of the classic *Animalium Cavernarum Catalogus* (Wolf, 1934-1938) that any attempt was made to present a checklist of cavernicolous organisms of the world. This work includes trogloxenes, troglophiles and troglobites.

No previous attempt has been made to publish a checklist of troglobitic organisms of the United States, although checklists of a few families and of several limited geographical areas are available. Dearolf (1937, 1941, 1953, 1956) has compiled lists of the invertebrate and vertebrate fauna found in North American caves, but these do not contain information on ranges nor are they necessarily complete. Individual state lists are too numerous to mention but none of these are limited to troglobites.

Troglobitic Tricladida have been described by Hyman (1937, 1945, 1954, 1956). Gates (1959) reviewed the earthworms of North America but did not include these organisms in any specific category. It would be difficult to determine the degree of adaptation of earthworms to the cave habitat. Hubricht (1941) and Smith (1957) have compiled lists of cavernicolous molluscans. The troglobitic forms are confined to the eastern and southeastern United States. Hubricht (1943) has also published a list of cavernicolous Amphipoda of the eastern United States. The cavernicolous Isopoda are to be found in the synopses of Van Name (1936, 1940, 1943) with additional species listed by Eberly (1954). The crayfish inhabiting caves are in need of a thorough study as many of the papers published since the authoritative work of Hobbs (1942) are at variance concerning range and nomenclature. Hubbell's monograph (1936) remains the standard work dealing with cavernicolous Orthoptera. A large number of papers have been published dealing with the classification of cavernicolous Coleoptera. The most recent significant papers dealing with the Carabidae are those of Jeannel (1949), Valentine (1942, 1952), Krekeler (1958) and Barr (1959, 1960). Park (1947, 1951, 1953, 1958) has discussed the classification of the Pselaphidae. Cavernicolous Diplopoda are listed in the general checklist of Chamberlin and Hoffman (1958) with additional species recorded by Causey (1959a, 1959b). The Amblyopsidae have been reviewed by Woods and Inger (1957). The nomenclature of cave-dwelling Plethodontidae is that of Schmidt (1953). Cavernicolous Chiroptera, all of which are trogloxenes, are treated in the recent work of Hall and Kelson (1959).

All species listed in this checklist are obligative cavernicoles. Hence, such common facultative forms as *Eurycea lucifuga, Plethodon glutinosus, Ceuthophilus stygius, Hadenoecus subterraneus* and *Meta menardii* are omitted. In the case of such naturally occurring hypogean taxa, it is difficult to determine whether the occurrence is obligative or facultative. Authenticated records of cavernicolous organisms, observed for the greater portion of their life cycle away from the cave (barring accidental or forced migration), have resulted in their exclusion from this list.

In the matter of distribution, the paucity of troglobites from certain limestone areas not subject to glaciation or flooding in the Pleistocene is indicative more of a lack of thorough collecting than an absence of life in the caves of these areas. Recent intensive collecting by T. C. Barr, Jr. and C. H. Krekeler through the Ohio and Mississippi valleys has disclosed many well-known caves with hitherto unknown troglobitic species. Another important factor limiting our knowledge of both the number of species and their ranges is lack of published data. The author knows of two species of troglobitic salamanders and at least eight species of Phalangida that have yet to be described. Many collections of cave material preserved in several of our larger museums have yet to be examined. The ranges listed are based on published records or amendations from personal observations of many investigators. It is hoped that presentation of the species and ranges

as now known will encourage those with additional observations to publish their data.

While some taxa remain undescribed, the status of others is dubious, especially with regard to synonomy. The Astacidae and Plethodontidae are particularly in need of further analysis. Confusion still exists on taxonomic differences between two genera of Asellidae, *Asellus* and *Caecidotea* (Chappuis, 1927; Miller, 1933). Use of the latter in this checklist is in keeping with the usage of more recent authors (Collinge, 1944; Mackin and Hubricht, 1940; and Levi, 1949).

Many have aided in the verification of the information listed. To name all who contributed to the compilation of this publication would necessitate several long paragraphs. Particular appreciation is expressed to the following for their assistance with the taxa noted: Dr. Thomas C. Barr, Jr., Catopidae, Campodeidae and Carabidae; Dr. Orlando Park, Pselaphidae; Dr. Kenneth Christiansen, Collembola; Dr. Libbie H. Hyman, Turbellaria; Dr. Clarence J. Goodnight, Phalangida; Dr. Willis J. Gertsch, Araneae; Dr. Nell Causey, Diplopoda; Dr. William Eberly, Decapoda. Dr. Robert E. Gordon has been helpful with pertinent suggestions throughout the preparation of the manuscript. The author, however, assumes full responsibility for any errors or omissions. This publication is part of a series that is planned to eventually include a checklist of all Nearctic troglobites.

PLATYHELMINTHES

TURBELLARIA

TRICLADIDA

Dendrocoelidae

Macrocotlya glandulosa Hyman

Macrocotyla glandulosa Hyman, 1956. Am. Mus. Novitates, no. 1808:9.

Type locality.—Unnamed cave, Rock Bridge, 5 miles south of Columbia, Boone Co., Missouri.

Range.—Known only from type locality.

Sorocelis americana Hyman

Sorocelis americana Hyman, 1939. Proc. U. S. Nat. Mus., 86:422.

Type locality.—Bat Cave, Adair Co., Oklahoma.

Range.—Caves of Oklahoma and Arkansas.

Kenkiidae

Kenkia rhynchida Hyman

Kenkia rhynchida Hyman, 1937. Trans. Am. Microscop. Soc., 56:456.

Type locality.—Malheur Cave, 15 miles west-by-north from Folly Farm, Harney Co., Oregon.

Range.—Known only from type locality.

Speophila buchanani Hyman

Speophila buchanani Hyman, 1937. Trans. Am. Microscop. Soc., 56:468.

Type locality.—Mammoth Cave, Edmonson Co., Kentucky.

Range.—Known only from type locality.

Speophila hoffmasteri Hyman

Speophila hoffmasteri Hyman, 1954. Proc. U. S. Nat. Mus., 103:570.

Type locality.—Blowing Cave, Pendleton Co., West Virginia.

Range.—Type locality and Mystic Cave, Pendleton Co., West Virginia.

Speophila hubrichti Hyman

Speophila hubrichti Hyman, 1945. Am. Midl. Nat., 34:479.

Type locality.—Morrison's Cave, 2 miles south of Burksville, Monroe Co., Illinois.

Range.—Caves of Illinois and Missouri.

Speophila pricei Hyman

Speophila pricei Hyman, 1937. Trans. Am. Microscop. Soc., 56:462.

Type locality.—Refton Cave, 1 mile northwest of Refton, Lancaster Co., Pennsylvania.

Range.—Caves of Pennsylvania.

Sphalloplana alabamensis Hyman

Sphalloplana alabamensis Hyman, 1956. Am. Midl. Nat., 34:476.

Type locality.—Sauta Cave, Lim Rock, Jackson Co., Alabama.

Range.—Type locality; Meredith Cave, Campbell Co.; Harve Petty Cave, Putnam Co.; Creeping Cave, Van Buren Co., Tennessee.

Sphalloplana georgiana Hyman

Sphalloplana georgiana Hyman, 1954. Proc. U. S. Nat. Mus., 103:566.

Type locality.—Waterfall Cave, Trenton, Walker Co., Georgia.

Range.—Known only from type locality.

Sphalloplana mohri Hyman

Sphalloplana mohri Hyman, 1939. Trans. Am. Microscop. Soc., 58:277.

Type locality.—Ezell's Cave, San Marcos, Hays, Co., Texas.

Range.—Caves of Texas, Oklahoma, Arkansas and Missouri.

Sphalloplana kansensis Hyman

Sphalloplana kansensis Hyman, 1945. Am. Midl. Nat., 34:478.

Type locality.—Purity Springs, near Augusta, Butte Co., Kansas.

Range.—Known only from type locality.

Sphalloplana percoeca (Packard)

Dendrocoelum percoeca Packard, 1880. Zoology for High Schools and Colleges: 142.

Sphalloplana percoeca (Packard) de Beauchamp, 1931. Arch. Zool. exp. Gen., 71:323.

Type locality.—Mammoth Cave, Edmonson Co., Kentucky.

Range.—Edmonson and Hart Cos., Kentucky.

Sphalloplana virginiana Hyman

Sphalloplana virginiana Hyman, 1945. Am. Midl. Nat., 34:477.

Type locality.—Showhalter's Cave, near Lexington, Rockbridge Co., Virginia.

Range.—Known only from type locality.

Planariidae

Phagocata cavernicola Hyman

Phagocata cavernicola Hyman, 1954. Proc. U. S. Nat. Mus., 103:563.

Type locality.—Evac Cave, near Hillside, Westmoreland Co., Pennsylvania.

Range.—Type locality and possibly Conoduginet Cave, Cumberland Co., Pennsylvania.

Phagocata subterranea Hyman

Phagocata subterranea Hyman, 1937. Trans. Am. Microscop. Soc., 56:474.

Type locality.—Donaldson's Cave, 4 miles east of Mitchell, Lawrence Co., Indiana.

Range.—Caves of Lawrence and Monroe Cos., Indiana.

ARTHROPODA

CRUSTACEA

AMPHIPODA

Gammaridae

Allocrangonyx pellucidus (Mackin)

Niphargus pellucidus Mackin, 1935. Trans. Am. Microscop. Soc., 54:42.

Allocrangonyx pellucidus (Mackin) Schellenberg, 1936. Mitt. Zool. Mus. Berlin, 22(1):33.

Type locality.—Bird's Mill Spring, southern Pontotoc Co., Oklahoma.

Range.—Type locality; Phelps and Pulaski Cos., Missouri; and Murray Co., Oklahoma.

Apocrangonyx lucifugus (O. P. Hay)

Crangonyx lucifugus O. P. Hay, 1882. Am. Nat., 16:144.

Apocrangonyx lucifugus (O. P. Hay) Stebbing, 1899. Trans. Linn. Soc. London, II, 7:422.

Type locality.—Well in Abingdon, Knox Co., Illinois.

Range.—Known only from type locality.

Apocrangonyx subtilis Hubricht

Apocrangonyx subtilis Hubricht, 1943. Am. Midl. Nat., 29:711.

Type locality.—Small seep near Bat Cave, 5 miles southwest of Pomona, Jackson Co., Illinois.

Range.—Jackson, Jersey and Union Cos., Illinois.

Bactrurus brachycaudus Hubricht and Mackin

Bactrurus brachycaudus Hubricht and Mackin, 1940. Am. Midl. Nat., 23:201.

Type locality.—A walled spring, Keifer Creek, 0.6 mile northwest of Fern Glen, St. Louis Co., Missouri.

Range.—Illinois and Missouri.

Bactrurus hubrichti Shoemaker

Bactrurus hubrichti Shoemaker, 1945. J. Wash. Acad. Sci., 35:27.

Type locality.—A well, Topeka, Shawnee Co., Kansas.

Range.—Eastern Kansas and Oklahoma.

Bactrurus mucronatus (Forbes)

Crangonyx mucronatus Forbes, 1876. Bull. Ill. State Lab. Nat. Hist., 1:6.

Bactrurus mucronatus (Forbes) W. P. Hay, 1902. Proc. U. S. Nat. Mus., 25:429.

Type locality.—Normal, McLean Co., Illinois.

Range.—Iowa, Missouri, Illinois, Indiana and Ohio.

Crangonyx antennatus Packard

Crangonyx antennatus Packard, 1881. Am. Nat., 15:880.

Type locality.—Nickajack Cave, Shellmound, Marion Co., Tennessee.

Range.—Virginia, Tennessee and Alabama.

Crangonyx dearolfi Shoemaker

Crangonyx dearolfi Shoemaker, 1942. Smithsonian Misc. Coll., 101:20.

Type locality.—Hobo Cave, Wernersville, Berks Co., Pennsylvania.

Range.—Known only from type locality.

Crangonyx forbesi (Hubricht and Mackin)

Eucrangonyx forbesi Hubricht and Mackin, 1940. Am. Midl. Nat., 23:196.

Crangonyx forbesi (Hubricht and Mackin) Hubricht, 1943. Am. Midl. Nat., 29:689.

Type locality.—A spring, Osage Golf Course, Kirkwood, St. Louis Co., Missouri.

Range.—Illinois, Missouri, Arkansas and Oklahoma.

Crangonyx gracilis packardi Smith

Crangonyx packardi Smith, 1888. Mem. Nat. Acad. Sci., 4:35.

Eucrangonyx packardi (Smith) Stebbing, 1899. Trans. Linn. Soc. London, II, 7:423.

Crangonyx gracilis packardi Smith, Hubricht, 1943. Am. Midl. Nat., 29:691.

Type locality.—Shiloh Cave, 2 miles east of Fayetteville, Lawrence Co., Indiana.

Range.—Indiana, Kentucky and Kansas.

Crangonyx hobbsi Shoemaker

Crangonyx hobbsi Shoemaker, 1941. Charleston Mus. Leaflet no. 16:9.

Type locality.—A well, 50 feet deep, 1.5 miles northeast of Chiefland, Levy Co., Florida.

Range.—Known only from type locality.

Crangonyx obliquus (Hubricht and Mackin)

Eucrangonyx obliquus Hubricht and Mackin, 1940. Am. Midl. Nat., 23:195.

Crangonyx obliquus (Hubricht and Mackin) Hubricht, 1943. Am. Midl. Nat., 29:689.

Type locality.—Small creek west of the college chapel, Clarksville, Johnson Co., Arkansas.

Range.—Eastern United States and southern Canada.

Gammarus acherondytes Hubricht and Mackin

Gammarus acherondytes Hubricht and Mackin, 1940. Am. Midl. Nat., 23:192.

Type locality.—Morrison's Cave, 2 miles south of Burksville, Monroe Co., Illinois.

Range.—Caves in Monroe Co., Illinois.

Gammarus minus Say

Gammarus minus Say, 1818. J. Acad. Nat. Sci. Phila., 1:373.

Type locality.—A spring, 1 mile west of Exton, Chester Co., Pennsylvania.

Range.—Pennsylvania, West Virginia, Virginia, Indiana, Kentucky, Tennessee, Alabama, Arkansas and Oklahoma.

Gammarus pseudolimnaeus Bousfield

Gammarus pseudolimnaeus Bousfield, 1958. Can. Field Nat., 72:74.

Type locality.—Rideau River, below Hog's Back, Ottawa, Ontario, Canada.

Range.—St. Lawrence River drainage and upper Mississippi River drainage as far south as northern Arkansas.

Gammarus troglophilus Hubricht and Mackin

Gammarus troglophilus Hubricht and Mackin, 1940. Am. Midl. Nat., 23:189.

Type locality.—Morrison's Cave, 2 miles south of Burksville, Monroe Co., Illinois.

Range.—Caves and springs of Illinois and Missouri.

Stygobromus exilis Hubricht

Crangonyx vitreus (Cope) Holmes, 1909. Trans. Wisc. Acad. Sci., 16:78.

Stygobromus exilis Hubricht, 1943. Am. Midl. Nat., 29:697.

Type locality.—Mammoth Onyx Cave, Hart Co., Kentucky.

Range.—Hart and Edmonson Cos., Kentucky; Blount and Hamilton Cos., Tennessee; Bibb Co., Alabama.

Stygobromus heteropodus Hubricht

Stygobromus heteropodus Hubricht, 1943. Am. Midl. Nat., 29:701.

Type locality.—Pickle Springs, head of Pickle Creek, Genevieve Co., Missouri.

Range.—Known only from type locality.

Stygobromus hubbsi Shoemaker

Stygobromus hubbsi Shoemaker, 1942. Occ. Pap. Mus. Zool., Univ. Mich., no. 466:1.

Type locality.—Malheur Cave, Harney Co., Oregon.

Range.—Known only from type locality.

Stygobromus iowae Hubricht

Stygobromus iowae Hubricht, 1943. Am. Midl. Nat., 29:703.

Type locality.—A spring, 0.7 miles north of Fayette, Fayette Co., Iowa.

Range.—Known only from type locality.

Stygobromus mackini Hubricht

Stygobromus mackini Hubricht, 1943. Am. Midl. Nat., 29:695.

Type locality.—Sikes Cave, 4.5 miles north of Lebanon, Russell Co., Virginia.

Range.—Type locality; Chimney Cave, Tazewell Co., Virginia, and Indian Cave, Grainger Co., Tennessee.

Stygobromus onondagaensis (Hubricht and Mackin)

Crangonyx onondagaensis Hubricht and Mackin, 1940. Am. Midl. Nat., 23:202.

Stygobromus onondagaensis (Hubricht and Mackin) Hubricht, 1943. Am. Midl. Nat., 29:699.

Type locality.—Onondaga Cave, 5 miles southeast of Leasburg, Crawford Co., Missouri.

Range.—Missouri and Kansas.

Stygobromus putealis (Holmes)

Crangonyx putealis Holmes, 1908. Trans. Wisc. Acad. Sci., 16:77.

Stygobromus putealis (Holmes) Schellenberg, 1936. Mitt. Zool. Mus. Berlin, 22:37.

Type locality.—Well, Rosendale, Fond du Lac Co., Wisconsin.

Range.—Fond du Lac Co., Wisconsin.

Stygobromus smithi Hubricht

Stygobromus smithi Hubricht, 1943. Am. Midl. Nat., 29:703.

Type locality.—A well, Woodstock, Bibb Co., Alabama.

Range.—Bibb and Tuscaloosa Cos., Alabama.

Stygobromus spinosus (Hubricht and Mackin)

Crangonyx spinosus Hubricht and Mackin, 1940. Am. Midl. Nat., 23:203.

Stygobromus spinosus (Hubricht and Mackin) Hubricht, 1943. Am. Midl. Nat., 29:697.

Type locality.—A spring near Hawksbill Mountain, Skyline Drive, Shenandoah National Park, Madison Co., Virginia.

Range.—Type locality and Luray Caverns, Page Co., Virginia.

Stygobromus vitreus Cope

Stygobromus vitreus Cope, 1872. Am. Nat., 6:422.

Type locality.—Mammoth Cave, Edmonson Co., Kentucky.

Range.—Kentucky, Alabama and Tennessee.

Stygonectes balconis Hubricht

Stygonectes balconis Hubricht, 1943. Am. Midl. Nat., 29:707.

Type locality.—Boyett's Cave, 14 miles northwest of San Marcos, Hays Co., Texas.

Range.—Type locality and Cave-Without-A-Name, 11 miles NE. of Boerne, Kendall Co., Texas.

Stygonectes flagellatus (Benedict)

Crangonyx flagellatus Benedict, 1896. Proc. U. S. Nat. Mus., 18:616.

Stygonectes flagellatus (Benedict) Hay, 1902. Proc. U. S. Nat. Mus., 25:429.

Type locality.—Artesian well, San Marcos, Hays Co., Texas.

Range.—Hays Co., Texas.

Synpleonia alabamensis (Stout)

Crangonyx alabamensis Stout, 1911. Pomona Coll. J. Entomol., 3:569.

Synpleonia alabamensis (Stout) Schellenberg, 1936. Mitt. Zool. Mus. Berlin, 22:40.

Type locality.—A well, 1 mile east of post office, Auburn, Lee Co., Alabama.

Range.—Known only from type locality.

Synpleonia americana (Mackin)

Boruta americana Mackin, 1935. Trans. Am. Microscop. Soc., 54:46.

Synpleonia americana (Mackin) Schellenberg, 1936. Mitt. Zool. Mus. Berlin, 22:40.

Type locality.—Crevices in San Bois Mountains near Wilburton, Latimer Co., Oklahoma.

Range.—Missouri, Arkansas and Oklahoma.

Synpleonia clantoni Creaser

Synpleonia clantoni Creaser, 1934. Occ. Pap. Mus. Zool., Univ. Mich., no. 282:2.

Type locality.—A well, 4 miles southeast of Ottawa, Franklin Co., Kansas.

Range.—Missouri, Kansas, Arkansas and Oklahoma.

Synpleonia emarginata Hubricht

Synpleonia emarginata Hubricht, 1943. Am. Midl. Nat., 29:707.

Type locality.—Organ Cave, Greenbrier Co., West Virginia.

Range.—Type locality and Hayes Cave, Greenbrier Co., West Virginia.

Synpleonia hayi Hubricht and Mackin.

Synpleonia hayi Hubricht and Mackin, 1940. Am. Midl. Nat., 23:205.

Type locality.—A spring, south end of National Zoological Park, Washington, D. C.

Range.—Type locality and caves of Fayette and Centre Cos., Pennsylvania.

Synpleonia pizzinii Shoemaker

Synpleonia pizzinni Shoemaker, 1938. Proc. Biol. Soc. Wash., 51:137.

Type locality.—Wetzel's Spring, Grover Archbold Park, just west of Georgetown, D. C.

Range.—District of Columbia, Fairfax Co., Virginia and southern Pennsylvania.

Synpleonia tenuis (S. I. Smith)

Crangonyx tenuis S. I. Smith, 1874. Rept. U. S. Fish Comm., 1872-3, 2:656.

Synpleonia tenuis (S. I. Smith) Shoemaker, 1938. Proc. Biol. Soc. Wash., 51:140.

Type locality.—Wells in Middletown, Middlesex Co., Connecticut.

Range.—New York, Connecticut south to Virginia.

ISOPODA

Asellidae

Asellus adenta Mackin and Hubricht

Asellus adenta Mackin and Hubricht, 1940. Trans. Am. Microscop. Soc., 50:396.

Type locality.—Cave located 15 miles south of Mountain View, Kiowa Co., Oklahoma.

Range.—Known only from type locality.

Asellus brevicauda Forbes

Asellus brevicauda Forbes, 1876. Bull. Ill. Mus. Nat. Hist., no. 1:8.

Type locality.—Southern Illinois.

Range.—Southern Illinois, Missouri, Tennessee and Arkansas.

Asellus californicus Miller

Asellus californicus Miller, 1933. Univ. Calif. Publ. Zool., 39:97.

Type locality.—A well near Kelseyville, Lake Co., California.

Range.—Known only from type locality.

Caecidotea acuticarpa Mackin and Hubricht

Caecidotea acuticarpa Mackin and Hubricht, 1940. Trans. Am. Microscop. Soc., 59:394.

Type locality.—Byrd's Mill Spring, Pontotoc Co., Oklahoma.

Range.—Springs, wells and caves in the Arbuckle Uplift in Pontotoc, Johnson, Murray and Seminole Cos., Oklahoma.

Caecidotea alabamensis Stafford

Caecidotea alabamensis Stafford, 1911. Pomona Coll. J. Entomol., 3:572.

Type locality.—A well in Auburn, Lee Co., Alabama.

Range.—Known only from type locality.

Caecidotea antricola Creaser
Caecidotea antricola Creaser, 1931. Occ. Pap. Mus. Zool., Univ. Mich., 222:1.
Type locality.—River Cave, Hahatonka, Camden Co., Missouri.
Range.—Type locality and St. Louis Co., Missouri.

Caecidotea conestogensis Levi
Caecidotea conestogensis Levi, 1949. Notulae Nat., no. 220:3.
Type locality.—Hammer Creek, 2 miles from Buffalo Springs, Lebanon Co., Pennsylvania.
Range.—Known only from type locality.

Caecidotea dimorpha Mackin and Hubricht
Caecidotea dimorpha Mackin and Hubricht, 1940. Trans. Am. Microscop. Soc., 59:385.
Type locality.—Seep, 0.5 mile south of Greenville, Wayne Co., Missouri.
Range.—Type locality and small spring, 1.5 miles SW. of Olyphant, Jackson Co., Arkansas.

Caecidotea hobbsi (Maloney)
Asellus hobbsi Maloney, 1939. Proc. U. S. Nat. Mus., 96:457.
Caecidotea hobbsi (Maloney) Van Name, 1943. Bull. Am. Mus. Nat. Hist., 80:321.
Type locality.—Dudley Cave, Gainesville, Alachua Co., Florida.
Range.—Type locality and Calhoun Co., Florida.

Caecidotea macropropoda Chase and Blair
Caecidotea macropropoda Chase and Blair, 1937. Am. Midl. Nat., 18:221.
Type locality.—Small streams in unnamed cave, 5 miles south of Kansas, Delaware Co., Oklahoma.
Range.—Known only from type locality.

Caecidotea nickajackenis Packard
Caecidotea nickajackensis Packard, 1881. Am. Nat., 15:879.
Type locality.—Nickajack Cave, Shellmound, Marion Co., Tennessee.
Range.—Type locality and Metcalf, Thomas Co., Georgia.

Caecidotea oculata Mackin and Hubricht
Caecidotea oculata Mackin and Hubricht, 1940. Trans. Am. Microscop. Soc., 59:395.
Type locality.—Springs in Rich Mountain, Rich Mountain Station, Polk Co., Arkansas.
Range.—Ouachita Mountain Uplift in Polk Co., Arkansas; Latimer and Leflore Cos., Oklahoma.

Caecidotea ozarkana Chase and Blair
Caecidotea ozarkana Chase and Blair, 1937. Am. Midl. Nat., 18:221.
Type locality.—Spring, 5 miles south of Kansas, Delaware Co., Oklahoma.
Range.—Known only from type locality.

Caecidotea packardi Mackin and Hubricht
Caecidotea packardi Mackin and Hubricht, 1940. Trans. Am. Microscop. Soc., 59:388.
Type locality.—Morrison's Cave, 2 miles south of Burksville, Monroe Co., Illinois.
Range.—Type locality and caves of St. Clair Co., Illinois.

Caecidotea pricei Levi
Caecidotea pricei Levi, 1949. Notulae Nat., no. 220:2.
Type locality.—Refton Cave, Lancaster Co., Pennsylvania.
Range.—Known only from type locality.

Caecidotea richardsonae Hay
Caecidotea richardsonae Hay, 1901. Proc. Biol. Soc. Wash., 14:180.
Type locality.—Nickajack Cave, Shellmound, Marion Co., Tennessee.
Range.—Known only from type locality.

Caecidotea smithii Ulrich
Caecidotea smithii Ulrich, 1902. Trans. Am. Microscop. Soc., 23:93.
Type locality.—Subterranean stream near San Marcos, Hays Co., Texas.
Range.—Known only from type locality.

Caecidotea spatulata Mackin and Hubricht
Caecidotea spatulata Mackin and Hubricht, 1940. Trans. Am. Microscop. Soc., 59:392.
Type locality.—Swales, 1 mile south of Falling Spring, St. Clair Co., Illinois.
Range.—Type locality; St. Louis and Boone Cos., Missouri.

Caecidotea stiladactyla Mackin and Hubricht
Caecidotea stiladactyla Mackin and Hubricht, 1940. Trans. Am. Microscop. Soc., 59:386.
Type locality.—Spring, 3.5 miles south of Jasper, Newton Co., Arkansas.
Range.—Newton and Boone Cos., Arkansas.

Caecidotea stygia Packard
Caecidotea stygia Packard, 1871. Am. Nat., 5:752.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Kentucky, Indiana, Illinois, Pennsylvania and Virginia.

Cirolanidae

Cirolanides texensis Benedict
Cirolanides texensis Benedict, 1896. Proc. U. S. Nat. Mus., 18:616.
Type locality.—Artesian well at San Marcos, Hays Co., Texas.
Range.—Known only from type locality.

Ligiidae

Ligidium kofoidi Maloney
Ligidium koifoidi Maloney, 1930. Univ. Calif. Publ. Zool., 23:291.
Type locality.—Potter Creek Cave, Shasta Co., California.
Range.—Known only from type locality.

Trichoniscidae

Amerigoniscus henroti Vandel
Amerigoniscus henroti Vandel, 1950. Arch. Zool. exp. Gen., 87:191.
Type locality.—Gillie's Cave, Lee Co., Virginia.
Range.—Known only from type locality.

Brackenridgia cavernarum Ulrich
Brackenridgia cavernarum Ulrich, 1902. Trans. Am. Microscop. Soc., 23:90.
Type locality.—Ezell's Cave, near San Marcos, Hays Co., Texas.
Range.—Caves of Hays Co., Texas, and Bat Cave, Eddy Co., New Mexico.

Miktoniscus racovitzai Vandel
Miktoniscus racovitzai Vandel, 1950. Arch. Zool. exp. Gen., 87:192.
Type locality.—Luray Caverns, Luray, Page Co., Virginia.
Range.—Known only from type locality.

DECAPODA

Astacidae

Cambarus cahni Rhoades
Cambarus cahni Rhoades, 1941. Proc. U. S. Nat. Mus., 91:146.
Type locality.—Belgreen Cave, Franklin Co., Alabama.
Range.—Known only from type locality.

Cambarus cryptodytes Hobbs
Cambarus cryptodytes Hobbs, 1941. Am. Midl. Nat., 26:110.
Type locality.—A well, 2 miles south of Graceville, Jackson Co., Florida.
Range.—Known only from type locality.

Cambarus hamulatus (Cope and Packard)
Orconectes hamulatus Cope and Packard, 1881. Am. Nat., 15:881.
Cambarus hamulatus (Cope and Packard) Faxon, 1884. Proc. Am. Acad. Arts and Sci., 20:145.
Type locality.—Nickajack Cave, Shellmound, Marion Co., Tennessee.
Range.—Caves of Marion and Franklin Cos., Tennessee.

Cambarus hubrichti Hobbs
Cambarus hubrichti Hobbs, 1952. Am. Midl. Nat., 48:690.
Type locality.—Lewis Cave, 15 miles northwest of Doniphan, Ripley Co., Missouri.
Range.—Type locality; Dewey Minick Cave, Oregon Co.; Midco Cave, Carter Co., Missouri.

Cambarus jonesi Hobbs and Barr
Cambarus jonesi Hobbs and Barr, 1960. Am. Midl. Nat., 64:19.
Type locality.—Cave Spring Cave, 12.1 miles northwest of Valhermosa, Morgan Co., Alabama.
Range.—Type locality and Shelta Cavern, Huntsville, Madison Co., Alabama.

Cambarus setosus Faxon
Cambarus setosus Faxon, 1889. Bull. Mus. Comp. Zool., 17:237.
Cambarus ayersii Steele, Hobbs and Barr, 1960. Am. Midl. Nat., 64:27.
Type locality.—Wilson's Cave, Jasper Co., Missouri.
Range.—Caves of James River drainage, southwestern Missouri.

Orconectes pellucidus pellucidus (Tellkampf)
Astacus pellucidus Tellkampf, 1844. Arch. Anat. Physiol. u. Wissench. Med., p. 383.
Cambarus pellucidus (Tellkampf) Hagen, 1870. Ill. Cat. Mus. Comp. Zool. 3:5.
Orconectes pellucidus pellucidus (Tellkampf) Hobbs, 1942. Am. Midl. Nat., 28:352.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Caves of northern Kentucky and southern Indiana.

Orconectes pellucidus australis (Rhoades)
Cambarus pellucidus australis Rhoades, 1941. Proc. U. S. Nat. Mus., 91:142.
Orconectes pellucidus australis (Rhoades) Hobbs, 1942. Am. Midl. Nat., 28:353.
Type locality.—Shelta Cave, Huntsville, Madison Co., Alabama.
Range.—Known only from type locality.

Orconectes pellucidus inermis Cope
Orconectes inermis Cope, 1872. Am. Nat., 6:420.
Orconectes pellucidus inermis Cope, Rhoades, 1959. Am. Midl. Nat., 61:401.
Type locality.—Wyandotte Cavern, Crawford Co., Indiana.
Range.—Caves of southern Indiana.

Orconectes pellucidus packardii Rhoades
Orconectes pellucidus packardii Rhoades, 1944. Am. Midl. Nat., 31:121.
Type locality.—Cumberland Crystal Cave, Alpine, Pulaski Co., Kentucky.
Range.—Caves of Pulaski Co., Kentucky.

Procambarus acherontis Lonnberg
Procambarus acherontis Lonnberg, 1894. Proc. U. S. Nat. Mus., 89:387.
Type locality.—Cave near Palm Springs, Seminole Co., Florida.
Range.—Known only from type locality.

Procambarus lucifugus lucifugus Hobbs
Procambarus lucifugus lucifugus Hobbs, 1940. Proc. U. S. Nat. Mus., 89:398.
Type locality.—Gum Cave, 5 miles southwest of Floral City, Citrus Co., Florida.
Range.—Known only from type locality.
Procambarus lucifugus alachua Hobbs
Procambarus lucifugus alachua Hobbs, 1940. Proc. U. S. Nat. Mus., 89:402.
Type locality.—Hog Sink, 10 miles west of Gainesville, Alachua Co., Florida.
Range.—Known only from type locality.
Procambarus pallidus Hobbs
Procambarus pallidus Hobbs, 1940. Proc. U. S. Nat. Mus., 89:394.
Type locality.—Warrens Cave, 11 miles northwest of Gainesville, Alachua Co., Florida.
Range.—Known only from type locality.
Troglocambarus maclanei Hobbs
Troglocambarus maclanei Hobbs, 1942. Am. Midl. Nat., 28:345.
Type locality.—Squirrel Chimney Cave, 11 miles northwest of Gainesville, Alachua Co., Florida.
Range.—Caves of Alachua and Citrus Cos., Florida.
Atyidae
Palaemonias ganteri Hay
Palaemonias ganteri Hay, 1901. Proc. Biol. Soc. Wash., 14:180.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Known only from type locality.
Palaemonidae
Palaemonetes antrorum Benedict
Palaemonetes antrorum Benedict, 1896. Proc. U. S. Nat. Mus., 18:165.
Type locality.—Artesian well, San Marcos, Hays Co., Texas.
Range.—Caves in vicinity of San Marcos, Hays Co., Texas.
Palaemonetes cummingi Chace
Palaemonetes cummingi Chace, 1954. J. Wash. Acad. Sci., 44:319.
Type locality.—Squirrel Chimney Cave, 11 miles northwest of Gainesville, Alachua Co., Florida.
Range.—Known only from type locality.

MYRIAPODA

DIPLOPODA

Cambalidae
Cambala caeca Loomis
Cambala caeca Loomis, 1953. J. Wash. Acad. Sci., 43:417.
Type locality.—Sonora, Sutton Co., Texas.
Range.—Caves in Sutton Co., Texas.
Cambala captiosa Causey
Cambala captiosa Causey, 1959. Proc. Biol. Soc. Wash., 72:69.
Type locality.—Beck's Ranch Cave, 6 miles west of Round Rock, Williamson Co., Texas.
Range.—Known only from type locality.
Eclomus speobius (Chamberlin)
Eclytus speobius Chamberlin, 1952. Entomol. News, 63:11.
Eclomus speobius (Chamberlin) Chamberlin, 1952. Entomol. News, 63:71.
Type locality.—Wyatt Cave, Sonora, Sutton Co., Texas.
Range.—Known only from type locality.

Troglocambala loomsi Hoffman
Troglocambala loomsi Hoffman, 1956. Geol. Surv. Alabama, Mus. Pap. no. 35:10.
Type locality.—Turk's (Brooklyn) Cave, Conecuh Co., Alabama.
Range.—Known only from type locality.

Cleidogonidae

Dearolfia lusciosa Loomis
Dearolfia lusciosa Loomis, 1939. Bull. Mus. Comp. Zool., 86:178.
Type locality.—Seneca Caverns, Riverton, Pendleton Co., West Virginia.
Range.—Caves in Pendleton and Pocahontas Cos., West Virginia.

Pseudotremia cavernarum Cope
Pseudotremia cavernarum Cope, 1869. Proc. Am. Philos. Soc., 11:179.
Type locality.—Erhart's Cave, 5 miles east of Christianburg, Montgomery Co., Virginia.
Range.—Caves of Giles and Montgomery Cos., Virginia.

Pseudotremia eburnea Loomis
Pseudotremia eburnea Loomis, 1939. Bull. Mus. Comp. Zool., 86:174.
Type locality.—Cricket Cave, Rising Fawn, Walker Co., Georgia.
Range.—Known only from type locality.

Pseudotremia fulgida Loomis
Pseudotremia fulgida Loomis, 1943. Bull. Mus. Comp. Zool., 92:378.
Type locality.—Higginbotham Cave, 1.5 miles northwest of Frankford, Greenbrier Co., West Virginia.
Range.—Caves in northern Greenbrier Co., West Virginia.

Pseudotremia hobbsi Hoffman
Pseudotremia hobbsi Hoffman, 1950. J. Wash. Acad. Sci., 40:90.
Type locality.—Chestnut Ridge Cave, 2.5 miles northwest of Clifton Forge, Alleghany Co., Virginia.
Range.—Caves in upper James River system in Alleghany and Bath Cos., Virginia.

Pseudotremia indianae Chamberlin and Hoffman
Pseudotremia cavernarum (not Cope) Cook and Collins, 1895. Ann. New York Acad. Sci., 9:36.
Pseudotremia indianae Chamberlin and Hoffman, 1958. U. S. Nat. Mus. Bull., 212:95.
Type locality.—Wyandotte Cave, Crawford Co., Indiana.
Range.—Caves of southern Indiana.

Pseudotremia nodosa Loomis
Pseudotremia nodosa Loomis, 1939. Bull. Mus. Comp. Zool., 86:175.
Type locality.—English Cave, near Harrowgate, Claiborne Co., Tennessee.
Range.—Caves of the Lower Powell River drainage in Claiborne and Anderson Cos., Tennessee.

Pseudotremia simulans Loomis
Pseudotremia simulans Loomis, 1939. Bull. Mus. Comp. Zool., 86:170.
Type locality.—Simmon's Cave, Pendleton Co., West Virginia.
Range.—Known only from type locality.

Pseudotremia sodalis Loomis
Pseudotremia sodalis Loomis, 1939. Bull. Mus. Comp. Zool., 86:173.
Type locality.—Bat Cave, Carter Co., Kentucky.
Range.—Known only from type locality.

Pseudotremia sublevis Loomis
Pseudotremia sublevis Loomis, 1944. Psyche, 51:67.
Type locality.—Tawney's Cave, Newport, Giles Co., Virginia.
Range.—Caves of Giles and Montgomery Cos., Virginia.

Pseudotremia valga Loomis
Pseudotremia valga Loomis, 1943. Bull. Mus. Comp. Zool., 92:377.

Type locality.—King Solomon's Cave (Cudjo's Cave), Cumberland Gap, Lee Co., Virginia.
Range.—Known only from type locality.

Conotylidae

Conotyla bollmani (McNeil)
Trichopetalum bollmani McNeil, 1887. Proc. U. S. Nat. Mus., 10:330.
Conotyla bollmani (McNeil), Cook and Collins, 1895. Ann. New York Acad. Sci., 9:76.
Type locality.—Mayfield's Cave, Bloomington, Monroe Co., Indiana.
Range.—South and central Indiana.

Conotyla vaga Loomis
Conotyla vaga Loomis, 1939. Bull. Mus. Comp. Zool., 86:182.
Type locality.—South Temple Cave, Berks Co., Pennsylvania.
Range.—Eastern Pennsylvania south to northern Maryland.

Scoterpes austrinus austrinus Loomis
Scoterpes austrinus austrinus Loomis, 1943. Bull. Mus. Comp. Zool., 92:386.
Type locality.—Manitou Cave, 1 mile south of Fort Payne, De Kalb Co., Alabama.
Range.—Known only from type locality.

Scoterpes austrinus nudus Chamberlin
Scoterpes austrinus nudus Chamberlin, 1946. Entomol. News, 57:152.
Type locality.—Saltpeter Cave, 4 miles north of Kingston, Bartow Co., Georgia.
Range.—Known only from type locality.

Scoterpes copei (Packard)
Spirostrephon (Pseudotremia) copei Packard, 1871. Am. Nat., 5:748.
Scoterpes copei (Packard) Cope, 1872. Am. Nat., 6:414.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—West central Kentucky southeast to eastern Tennessee.

Scoterpes dendropus Loomis
Scoterpes dendropus Loomis, 1939. Bull. Mus. Comp. Zool., 86:181.
Type locality.—Marvel Cave, Stone Co., Missouri.
Range.—Type locality and Galena, Stone Co., Missouri.

Zygonopus whitei Ryder
Zygonopus whitei Ryder, 1881. Proc. U. S. Nat. Mus., 3:527.
Type locality.—Luray Caverns, Luray, Page Co., Virginia.
Range.—Caves of northwestern Virginia and Pendleton Co., West Virginia.

Erecethidae

Tingupa pallida Loomis
Tingupa pallida Loomis, 1939. Bull. Mus. Comp. Zool., 86:185.
Type locality.—River Cave, Hahatonka, Camden Co., Missouri.
Range.—Caves of eastern Missouri and adjacent western Illinois.

Lysiopetalidae

Tetracion jonesi jonesi Hoffman
Tetracion jonesi jonesi Hoffman, 1956. Geol. Surv. Alabama, Mus. Pap. no. 35:6.
Type locality.—Bat Cave, near Grant, Marshall Co., Alabama.
Range.—Known only from type locality.

Tetracion jonesi atraeum Hoffman
Tetracion jonesi atraeum Hoffman, 1956. Geol. Surv. Alabama, Mus. Pap. no. 35:8.
Type locality.—Barclay Cave, Madison Co., Alabama.
Range.—Known only from type locality.

Tetracion tennessieensis Causey
Tetracion tennessieensis Causey, 1959. J. Tenn. Acad. Sci., 34:236.
Type locality.—Cumberland Caverns, Warren Co., Tennessee.
Range.—Grundy and Warren Cos., Tennessee.

Nemasomidae
Ameractis satis Causey
Ameractis satis Causey, 1959. J. Tenn. Acad. Sci., 34:232.
Type locality.—Indian Cave, White Co., Tennessee.
Range.—Caves of White and Overton Cos., Tennessee.

Polydesmidae
Antriadesmus debilis Causey
Antriadesmus debilis Causey, 1959. J. Tenn. Acad. Sci., 34:231.
Type locality.—Walker Spring Cave, Wayne Co., Tennessee.
Range.—Known only from type locality.
Antriadesmus mollis Causey
Antriadesmus mollis Causey, 1959. J. Tenn. Acad. Sci., 34:230.
Type locality.—Cumberland Caverns, Warren Co., Tennessee.
Range.—Known only from type locality.
Brachydesmus cavicola Packard
Brachydesmus cavicola Packard, 1877. Bull. U. S. Geol. Geogr. Surv. (Hayden), 3:161.
Type locality.—Clinton's Cave, Tooele Co., Utah.
Range.—Known only from type locality.
Scytonotus cavernarum Bollman
Scytonotus cavernarum Bollman, 1887. Entomol. Am., 3:46.
Type locality.—Mayfield's Cave, Monroe Co., Indiana.
Range.—Known only from type locality.
Speodesmus bicornourus Causey
Speodesmus bicornourus Causey, 1959. Proc. Bio. Soc. Wash., 72:71.
Type locality.—Beck's Ranch Cave, 6 miles west of Round Rock, Williamson Co., Texas.
Range.—Known only from type locality.
Speodesmus echinourus Loomis
Speodesmus echinourus Loomis, 1939. Bull. Mus. Comp. Zool., 86:118.
Type locality.—Prassel Ranch Cave, Kendall Co., Texas.
Range.—Caves in Kerr, Kendall and Hays Cos., Texas.
Speorthus tuganbius Chamberlin
Speorthus tuganbius Chamberlin, 1952. Entomol. News, 63:12.
Type locality.—Carlsbad Caverns, Eddy Co., New Mexico.
Range.—Known only from type locality.

Striariidae
Striaria eldora Chamberlin
Striaria eldora Chamberlin, 1953. Entomol. News, 64:95.
Type locality.—Consumnes Cave, El Dorado Co., California.
Range.—Known only from type locality.
Striaria shastae Causey
Striaria shastae Causey, 1958. Proc. Biol. Soc. Wash., 71:182.
Type locality.—Samwel Cave, Shasta Co., California.
Range.—Known only from type locality.

Zosteractiidae
Zosteractis interminata Loomis
Zosteractis interminata Loomis, 1943. Bull. Mus. Comp. Zool., 92:395.
Type locality.—South Rankin Cave, 4 miles east of Eureka, St. Louis Co., Missouri.
Range.—Caves of St. Louis and St. Genevieve Cos., Missouri.

INSECTA

ORTHOPTERA

Gryllacrididae

Ceuthophilus longipes Caudell

Ceuthophilus longipes Caudell, 1924. Proc. Ent. Soc. Wash., 26:219.
Type locality.—Carlsbad Caverns, Eddy Co., New Mexico.
Range.—Known only from type locality.

COLLEMBOLA

Entomobryidae

Entomobrya troglodytes Christiansen

Entomobrya troglodytes Christiansen, 1958. Bull. Mus. Comp. Zool., 118:484.
Type locality.—Unnamed cave on property Sturgis Water Company, Sturgis, Meade Co., South Dakota.
Range.—Known only from type locality.

Lepidocytrus atropurpureus Packard

Lepidocytrus atropurpureus Packard, 1888. Mem. Nat. Acad. Sci., 4:66.
Type locality.—Diamond Cave, Edmonson Co., Kentucky.
Range.—Caves of Edmonson Co., Kentucky.

Parasinella cavernarum (Packard)

Degeeria cavernarum Packard, 1888. Mem. Nat. Acad. Sci., 4:66.
Entomobrya lucifuga Folsom, 1902. Psyche, 9:365.
Parasinella cavernarum (Packard) Bonet, 1942. Sciencia, 3:56.
Type locality.—New Wyandotte Cave, Crawford Co., Indiana.
Range.—Type locality and Bradford Cave, Crawford Co., Indiana.

Sinella hoffmani Wray

Sinella hoffmani Wray, 1952. Bull. Brooklyn Entomol. Soc., 47:95.
Type locality.—Lowmoor Quarry Cave, Allegheny Co., Virginia.
Range.—Known only from type locality.

Troglosinella hirsuta Delamare

Troglosinella hirsuta Delamare, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:121.
Type locality.—Tennessee Caverns, 5 miles west of Chattanooga, Hamilton Co., Tennessee.
Range.—Known only from type locality.

Troglosinella spinosa Delamare

Troglosinella spinosa Delamare, 1949. Notes. Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:122.
Type locality.—Aladdin's Cave, Madison Co., Alabama.
Range.—Known only from type locality.

Hypogastruridae

Hypogastrura lucifugus (Packard)

Lipura? lucifugus Packard, 1888. Mem. Nat. Acad. Sci., 4:65.
Hypogastrura lucifugus (Packard) Christiansen, 1960. Am. Midl. Nat., 64:43.
Type locality.—Wyandotte Caverns, Crawford Co., Indiana.
Range.—Known only from type locality.

Isotomidae

Folsomia cavicola (Banks)

Entomobrya cavicola Banks, 1897. Am. Nat., 31:380.
Folsomia cavicola (Banks) Christiansen, 1960. Am. Midl. Nat., 64:42.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Known only from type locality.

Oncopoduridae

Oncopodura cruciata Bonet

Oncopodura cruciata Bonet, 1943. Ann. Esc. Nat. Cienc. Biol., 3:141.

Type locality.—Morrison's Cave, Bozeman, Gallatin Co., Montana.

Range.—Known only from type locality.

Onychiuridae

Onychiurus obesus Mills

Onychiurus obesus Mills, 1934. Collembola of Iowa:35.

Type locality.—Bixby Ice Cave, Bixby State Park, Clayton Co., Iowa.

Range.—Known only from type locality.

Sminthuridae

Arrhopalites ferrugineus (Packard)

Smynthurus ferrugineus Packard, 1888. Mem. Nat. Acad. Sci., 4:67.

Arrhopalites ferrugineus (Packard) Christiansen, 1960. Am. Midl. Nat., 64:40.

Type locality.—New Market Cave, Rockingham Co., Virginia.

Range.—Type locality and Weyer's (Grand) Caverns, August Co., Virginia.

Arrhopalites mammouthia (Banks)

Smynthurus mammouthia Banks, 1897. Am. Nat., 31:381.

Arrhopalites mammouthia (Banks) Christiansen, 1960. Am. Midl. Nat., 64:40.

Type locality.—Mammoth Cave, Edmonson Co., Kentucky.

Range.—Known only from type locality.

Tomoceridae

Tomocerus brevimucronata Denis

Tomocerus brevimucronata Denis, 1928. Bull. Mus. Portici Lab. di Zool., 22:176.

Type locality.—Oregon Cave, Josephine Co., Oregon.

Range.—Known only from type locality.

Tomocerus pallidus Packard

Tomocerus plumbea var. pallidus Packard, 1888. Mem. Nat. Acad. Sci., 4:65.

Tomocerus pallidus Giovannoli, 1933. Am. Midl. Nat., 14:615.

Type locality.—Carter's Cave, Carter Co., Kentucky.

Range.—Caves of Carter Co., Kentucky.

Tritomurus californicus Folsom

Tritomurus californicus Folsom, 1916. Proc. U. S. Nat. Mus., 46:469.

Type locality.—Palser (?) Cave, Santa Clara Co., California.

Range.—Known only from type locality.

Tritomurus henroti Delamare

Tritomurus henroti Delamare, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:117.

Type locality.—Erhardt's Cave, Montgomery Co., Virginia.

Range.—Known only from type locality.

Tritomurus missus Mills

Tritomurus missus Mills, 1948. Ann. Entomol. Soc. Am., 41:178.

Type locality.—Grafton Cave, Jersey Co., Illinois.

Range.—Type locality and Eckert's Cave, Monroe Co., Illinois.

Tritomurus oregonensis Denis

Tritomurus oregonensis Denis, 1928. Bull. Portici Lab. di Zool., 22:178.

Type locality.—Oregon Cave, Josephine Co., Oregon.

Range.—Known only from type locality.

DIPLURA

Campodeidae

Plusiocampa fieldingi Condé

Plusiocampa fieldingi Condé, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:132.

Type locality.—McClung's Cave, near Maxwelton, Greenbrier Co., West Virginia.

Range.—Known only from type locality.

Plusiocampa henroti Condé

Plusiocampa henroti Condé, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:127.

Type locality.—Shelta Cave, Huntsville, Madison Co., Alabama.

Range.—Known only from type locality.

Plusiocampa jonesi Condé

Plusiocampa jonesi Condé, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:135.

Type locality.—Dunbar Cave, Clarksville, Montgomery Co., Tennessee.

Range.—Known only from type locality.

Plusiocampa nearctica Silvestri

Plusiocampa nearctica Silvestri, 1934. Arch. Zool. exp. Gen., 76:379.

Type locality.—Mammoth Cave, Edmonson Co., Kentucky.

Range.—Type locality and Indian Cave, Barren Co., Kentucky.

Plusiocampa valentinei Condé

Plusiocampa valentinei Condé, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:130.

Type locality.—Cave Spring Cave, near Berkeley, Madison Co., Alabama.

Range.—Type locality and Aladdin Cave, Madison Co., Alabama.

COLEOPTERA

Carabidae

Agonum (Rhadine) exile Barr and Lawrence

Agonum (Rhadine) exile Barr and Lawrence, 1960. Wasmann J. Biol., 18.

Type locality.—Cave near Helotes, northern Bexar Co., Texas.

Range.—Caves near Helotes and Camp Bullis, northern Bexar Co., Texas.

Agonum (Rhadine) infernale infernale Barr and Lawrence

Agonum (Rhadine) infernale Barr and Lawrence, 1960. Wasmann J. Biol., 18.

Agonum (Rhadine) infernale infernale Barr and Lawrence, Barr, 1960. Am. Midl. Nat., 64:55.

Type locality.—Malda Cave near Helotes, Bexar Co., Texas.

Range.—Type locality and Alzifar Cave, 11 miles northeast of Boerne, Kendall Co., Texas.

Agonum (Rhadine) infernale ewersi Barr

Agonum (Rhadine) infernale ewersi Barr, 1960. Am. Midl. Nat., 64:55.

Type locality.—Headquarters Cave, Camp Bullis, Bexar Co., Texas.

Range.—Known only from type locality.

Agonum (Rhadine) koepkei Barr

Agonum (Rhadine) koepkei Barr, 1960. Am. Midl. Nat., 64:56.

Type locality.—Schneider's Ranch Cave, 14 miles northeast of Boerne, Kendall Co., Texas.

Range.—Type locality and unnamed cave near Sisterdale, Kendall Co., Texas.

Agonum (Rhadine) longicolle Benedict

Rhadine longicollis Benedict, 1928. Pan-Pac. Entomol., 4:44.

Agonum (Rhadine) longicolle (Benedict) Csiki, 1931. Coleopterum Catalogus, Pars 115, Carabidae: Harpavline V:849.

Type locality.—Carlsbad Caverns, Eddy Co., New Mexico.
Range.—Caves of Carlsbad Caverns National Park, Eddy Co., New Mexico.

Agonum (Rhadine) specum Barr
Agonum (Rhadine) specum Barr, 1960. Am. Midl. Nat., 64:58.
Type locality.—Cave-Without-A-Name, Kendall Co., Texas.
Range.—Type locality, Cascade Caverns and Alzifar Cave, Kendall Co., Texas.

Agonum (Rhadine) subterraneum (Van Dyke)
Comstockia subterraneum Van Dyke, 1918. J. New York Entomol. Soc., 26:172.
Agonum (Rhadine) subterraneum (Van Dyke) Barr and Lawrence, 1960. Wasmann J. Biol., 18.
Type locality.—Sam Bass Cave, McNeil, Travis Co., Texas.
Range.—Known only from type locality.

Agonum (Rhadine) tenebrosum Barr
Agonum (Rhadine) tenebrosum Barr, Am. Midl. Nat., 64:57.
Type locality.—Wilson's Cave, 25 miles southwest of Hunt, Kerr Co., Texas.
Range.—Type locality and unnamed cave near Hunt, Kerr Co., Texas.

Ameroduvalius jeanneli jeanneli Valentine
Ameroduvalius jeanneli jeanneli Valentine, 1952. Geol. Survey Alabama, Mus. Pap. no. 34:27.
Type locality.—Sloan's Valley (Cassidy) Cave, 6 miles southeast of Burnside, Pulaski Co., Kentucky.
Range.—Caves of Pulaski and McCreary Cos., Kentucky.

Ameroduvalius jeanneli rockcastlei Valentine
Ameroduvalius jeanneli rockcastlei Valentine, 1952. Geol. Surv. Alabama, Mus. Pap. no. 34:29.
Type locality.—Rockcastle Saltpeter Cave, 4 miles north of Livingston, Rockcastle Co., Kentucky.
Range.—Known only from type locality.

Darlingtonea kentuckensis kentuckensis Valentine
Darlingtonea kentuckensis kentuckensis Valentine, 1952. Geol. Surv. Alabama, Mus. Pap. no. 34:22.
Type locality.—Richardson's Cave, 2.5 miles east of Somerset, Pulaski Co., Kentucky.
Range.—Caves of Pulaski, McCreary, Wayne and Clinton Cos., Kentucky, and Fentress Co., Tennessee.

Darlingtonea kentuckensis lexingtoni Valentine
Darlingtonea kentuckensis lexingtoni Valentine, 1952. Geol. Surv. Alabama, Mus. Pap. no. 34:24.
Type locality.—Rockcastle Saltpeter Cave, 4 miles north of Livingston, Rockcastle Co., Kentucky.
Range.—Known only from type locality.

Horologion speokoites Valentine
Horologion speokoites Valentine, 1932. Ann. Am. Entomol. Soc., 25:3.
Type locality.—Arbuckle Cave, Greenbrier Co., West Virginia.
Range.—Known only from type locality.

Neaphaenops tellkampfi tellkampfi (Erichson)
Anophthalmus tellkampfi Erichson, 1844. Mullers Arch. Anat. u. Phys., p. 384.
Neaphaenops tellkampfi (Erichson) Jeannel, 1920. Bull. Soc. Entomol. France, p. 154.
Neaphaenops tellkampfi tellkampfi (Erichson) Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:90.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.

Range.—Barren, Hart, southern Hardin and eastern Edmonson Cos., Kentucky.

Neaphaenops tellkampfi henroti Jeannel

Neaphaenops tellkampfi henroti Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:90.

Type locality.—Sig Shacklett Cave, 5 miles southwest of Garret, Meade Co., Kentucky.

Range.—Caves of Meade Co., Kentucky.

Neaphaenops tellkampfi meridionalis Barr

Neaphaenops tellkampfi meridionalis Barr, 1959. J. Tenn. Acad. Sci., 34:23.

Type locality.—Hoy Cave, 2 miles north of Franklin, Simpson Co., Kentucky.

Range.—Known only from type locality.

Nelsonites jonesei Valentine

Nelsonites jonesei Valentine, 1952. Geol. Surv. Alabama, Mus. Pap. no. 34:16.

Type locality.—Richardson's Cave, 2.5 miles east of Somerset, Pulaski Co., Kentucky.

Range.—Caves of Somerset area, Pulaski Co., Kentucky.

Nelsonites walteri Valentine

Nelsonites walteri Valentine, 1952. Geol. Surv. Alabama, Mus. Pap. no. 34:18.

Type locality.—Johnson Cave, 7 miles southwest of Monterey, Putnam Co., Tennessee.

Range.—Caves of Putnam, Overton, Fentress, White and Van Buren Cos., Tennessee.

Pseudanophthalmus alabamae Valentine

Pseudanophthalmus alabamae Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:273.

Type locality.—Manitou Cave, 1.5 miles southwest of Fort Payne, De Kalb Co., Alabama.

Range.—Known only from type locality.

Pseudanophthalmus audax Horn

Pseudanophthalmus audax Horn, 1883. Trans. Am. Entomol. Soc., 10:270.

Type locality.—Ronald's Cave, Hart Co., Kentucky.

Range.—Known only from type locality.

Pseudanophthalmus barberi Jeannel

Pseudanophthalmus barberi Jeannel, 1928. L'Abeille, 35:138.

Type locality.—Rockhaven Cave, 8 miles east-by-northeast of Brandenburg, Meade Co., Kentucky.

Range.—Caves of Meade Co., Kentucky.

Pseudanophthalmus ciliaris ciliaris Valentine

Pseudanophthalmus ciliaris Valentine, 1937. J. Elisha Mitchell Sci. Soc., 53:95.

Pseudanophthalmus ciliaris ciliaris Valentine, Barr, 1959. J. Tenn. Acad. Sci., 34:6.

Type locality.—Dunbar Cave, 3 miles east of Clarksville, Montgomery Co., Tennessee.

Range.—Robertson and Montgomery Cos., Tennessee and eastern Christian Co., Kentucky.

Pseudanophthalmus ciliaris colemanensis Barr

Pseudanophthalmus ciliaris colemanensis Barr, 1959. J. Tenn. Acad. Sci., 34:6.

Type locality.—Coleman Cave, 8 miles west of Clarksville, Montgomery Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus ciliaris loganensis Barr

Pseudanophthalmus ciliaris loganensis Barr, 1959. J. Tenn. Acad. Sci., 34:7.

Type locality.—Cook Cave, 1 mile east of Adairville, Logan Co., Kentucky.

Range.—Caves of the upper Red River Valley, Kentucky and Tennessee.

Pseudanophthalmus cumberlandus Valentine

Pseudanophthalmus cumberlandus Valentine, 1937. J. Elisha Mitchell Sci. Soc., 53:96.

Type locality.—Piper Cave, Monoville, Smith Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus digitus Valentine

Pseudanophthalmus digitus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:270.

Type locality.—Crystal City Caves (Tennessee Caverns), 5 miles west of Chattanooga, Hamilton Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus emersoni Krekeler

Pseudanophthalmus emersoni Krekeler, 1958. Am. Midl. Nat., 59:176.

Type locality.—Donnehue's Cave, 1 mile southwest of Bedford, Lawrence Co., Indiana.

Range.—Known only from type locality.

Pseudanophthalmus engelhardti (Barber)

Anophthalmus engelhardti Barber, 1928. J. Wash. Acad. Sci., 18:195.

Pseudanophthalmus engelhardti (Barber) Jeannel, 1928. L'Abeille, 35:130.

Type locality.—English Cave, 3 miles south of Cumberland Gap, Claiborne Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus eremita (Horn)

Anophthalmus eremita Horn, 1871. Trans. Am. Entomol. Soc., 3:325.

Pseudanophthalmus eremita (Horn) Barr, 1960. Am. Midl. Nat., 63:308.

Type locality.—Wyandotte Cave, Crawford Co., Indiana.

Range.—Type locality and Langdon's Cave, Harrison Co., Indiana.

Pseudanophthalmus fuscus fuscus Valentine

Pseudanophthalmus fuscus fuscus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:254.

Type locality.—Coffman's Cave, Greenbrier Co., West Virginia.

Range.—Caves of northern Greenbrier Co., West Virginia.

Pseudanophthalmus fuscus constrictus Valentine

Pseudanophthalmus fuscus constrictus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:267.

Type locality.—Organ Cave, Ronceverte, Greenbrier Co., West Virginia.

Range.—Caves of southern Greenbrier Co., West Virginia.

Pseudanophthalmus gracilis Valentine

Pseudanophthalmus gracilis Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:253.

Type locality.—Tawney's Cave, Newport, Giles Co., Virginia.

Range.—Known only from type locality.

Pseudanophthalmus grandis grandis Valentine

Pseudanophthalmus grandis grandis Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:254.

Type locality.—Higginbotham's Cave, Frankford, Greenbrier Co., West Virginia.

Range.—Caves of northern Greenbrier Co., West Virginia.

Pseudanophthalmus grandis elevatus Valentine
Pseudanophthalmus grandis elevatus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:265.
Type locality.—Organ Cave, Ronceverte, Greenbrier Co., West Virginia.
Range.—Caves of southern Greenbrier Co., West Virginia.

Pseudanophthalmus henroti Jeannel
Pseudanophthalmus henroti Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:69.
Type locality.—Arbuckle's Cave, Greenbrier, Co., West Virginia.
Range.—Known only from type locality.

Pseudanophthalmus hesperus Barr
Pseudanophthalmus hesperus Barr, 1959. J. Tenn. Acad. Sci., 34:15.
Type locality.—Bethel Cave, Perry Co., Tennessee.
Range.—Known only from type locality.

Pseudanophthalmus higginbothami Valentine
Pseudanophthalmus higginbothami Valentine, 1931. J. Elisha Mitchell Sci. Soc., 46:251.
Type locality.—Higginbotham's Cave, Frankford, Greenbrier Co., West Virginia.
Range.—Caves of northern Greenbrier Co., West Virginia.

Pseudanophthalmus hirsutus hirsutus Valentine
Pseudanophthalmus hirsutus hirsutus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:252.
Type locality.—King Solomon's Cave, Cumberland Gap, Claiborne Co., Tennessee.
Range.—Known only from type locality.

Pseudanophthalmus hirsutus delicatus Valentine
Pseudanophthalmus hirsutus delicatus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:270.
Type locality.—Gilly's Cave, 1 mile south of Pennington Gap, Lee Co., Virginia.
Range.—Known only from type locality.

Pseudanophthalmus hubbardi hubbardi (Barber)
Anophthalmus hubbardi Barber, 1928. J. Wash. Acad. Sci., 18:196.
Pseudanophthalmus hubbardi (Barber) Jeannel, 1928. L'Abeille, 35:130.
Pseudanophthalmus hubbardi hubbardi (Barber) Jeannel, 1931. Arch. Zool. exp. Gen., 71:450.
Type locality.—Luray Caverns, Luray, Page Co., Virginia.
Range.—Known only from type locality.

Pseudanophthalmus hubbardi avernus Valentine
Pseudanophthalmus hubbardi avernus Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:648.
Type locality.—Endless Caverns, Rockingham Co., Virginia.
Range.—Known only from type locality.

Pseudanophthalmus hubbardi limicola Jeannel
Pseudanophthalmus hubbardi limicola Jeannel, 1931. Arch. Zool. exp. Gen., 71:450.
Type locality.—Madden Cave, 1.5 miles northwest of New Market Station, Shenandoah Co., Virginia.
Range.—Known only from type locality.

Pseudanophthalmus hubbardi parvicollis Jeannel
Pseudanophthalmus hubbardi parvicollis Jeannel, 1931. Arch. Zool. exp. Gen., 71:450.
Type locality.—Battlefield Crystal Cave, 2 miles northeast of Strasburg, Shenandoah Co., Virginia.
Range.—Known only from type locality.

Pseudanophthalmus hubrichti Valentine

Pseudanophthalmus hubrichti Valentine, 1948. Geol. Surv. Alabama, Mus. Pap. no. 27:13.

Type locality.—Dougherty's Cave, 3 miles northwest of Lebanon, Russell Co., Virginia.

Range.—Known only from type locality.

Pseudanophthalmus hypertrichosis Valentine

Pseudanophthalmus hypertrichosis Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:266.

Type locality.—Martha Clarke Cave, 2 miles southwest of Hillsboro, Pocahontas Co., West Virginia.

Range.—Known only from type locality.

Pseudanophthalmus inexpectatus Barr

Pseudanophthalmus inexpectatus Barr, 1959. J. Tenn. Acad. Sci., 34:10.

Type locality.—White Cave, Edmonson Co., Kentucky.

Range.—Type locality and Mammoth Cave National Park, Edmonson Co., Kentucky.

Pseudanophthalmus intermedius Valentine

Neaphaenops intermedius Valentine, 1931. J. Elisha Mitchell Sci. Soc., 46:249.

Pseudanophthalmus intermedius Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:276.

Type locality.—Wonder Cave, Monteagle, Grundy Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus jonesi Valentine

Pseudanophthalmus jonesi Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:645.

Type locality.—Saltpeter Cave, Grassy Cove, Cumberland Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus lallemanti Jeannel

Pseudanophthalmus lallemanti Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:74.

Type locality.—General Davis Cave, Greenbrier Co., West Virginia.

Range.—Known only from type locality.

Pseudanophthalmus leonae Barr

Pseudanophthalmus leonae Barr, 1960. Am. Midl. Nat., 63:310.

Type locality.—Hert Hollow Cave, 2 miles southwest of Springville, Lawrence Co., Indiana.

Range.—Known only from type locality.

Pseudanophthalmus lodingi lodingi Valentine

Pseudanophthalmus lodingi lodingi Valentine, 1931. J. Elisha Mitchell Sci. Soc., 46:252.

Type locality.—Shelta Cave, Huntsville, Madison Co., Alabama.

Range.— Caves of northwestern Madison Co., Alabama.

Pseudanophthalmus lodingi aladdini Valentine

Pseudanophthalmus lodingi aladdini Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:637.

Type locality.—Aladdin Cave, upper end of Sharp Cove, Madison Co., Alabama.

Range.—Caves of the tributaries of the Flint and Paint Rock Rivers, north of the Tennessee River in Madison and Jackson Cos., Alabama.

Pseudanophthalmus lodingi aquaticus Valentine

Pseudanophthalmus lodingi aquaticus Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:638.

Type locality.—Cave Spring Cave, between Troy and Keel mountains, near Berkely, Madison Co., Alabama.

Range.—Known only from type locality.

Pseudanophthalmus lodingi distinguens Valentine

Pseudanophthalmus lodingi distinguens Valentine, 1948. Geol. Surv. Alabama, Mus. Pap. no. 27:12.

Type locality.—Inge Cave, 5.5 miles south of Trinity, Morgan Co., Alabama.

Range.—Known only from type locality.

Pseudanophthalmus lodingi fluviatilis Valentine

Pseudanophthalmus lodingi fluviatilis Valentine, 1948. Geol. Surv. Alabama, Mus, Pap. no. 27:12.

Type locality.—Rock House Cave, 1 mile south of Oleander, Marshall Co., Alabama.

Range.—Type locality and caves of Newsome Sinks, Morgan Co., Alabama.

Pseudanophthalmus lodingi fulleri Valentine

Pseudanophthalmus fulleri Valentine, 1932. J. Elisha Mitchell Sci. Soc., 37:272.

Pseudanophthalmus lodingi fulleri Valentine, 1948. Geol. Surv. Alabama, Mus. Pap. no. 27:10.

Type locality.—Tennessee Caverns, 5 miles west of Chattanooga, Hamilton Co., Tennessee.

Range.—Caves of Lookout Valley, in Hamilton Co., Tennessee, and Dade Co., Georgia.

Pseudanophthalmus lodingi humeralis Valentine

Pseudanophthalmus humeralis Valentine, 1931. J. Elisha Mitchell Sci. Soc., 46:253.

Pseudanophthalmus humeralis brevis Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:273.

Pseudanophthalmus lodingi brevis Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:641.

Pseudanophthalmus lodingi humeralis Valentine, Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:84.

Type locality.—Crystal Cave, Grundy Co., Tennessee.

Range.—Crystal and Wonder Caves, Monteagle, Grundy Co., Tennessee.

Pseudanophthalmus lodingi meridionalis Valentine

Pseudanophthalmus lodingi meridionalis Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:639.

Type locality.—Guntersville Caverns, 3 miles east of Guntersville, Marshall Co., Alabama.

Range.—Known only from type locality.

Pseudanophthalmus lodingi profundus Valentine

Pseudanophthalmus lodingi profundus Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:637.

Type locality.—Natural well, Monte Santo Mountain, Madison Co., Alabama.

Range.—Known only from type locality.

Pseudanophthalmus macradei Valentine

Pseudanophthalmus macradei Valentine, 1948. Geol. Surv. Alabama, Mus. Pap. no. 27:9.

Type locality.—Cumberland Caverns, Warren Co., Tennessee.

Range.—Caves of eastern Warren Co., Tennessee.

Pseudanophthalmus menestriesi Motschoulsky

Pseudanophthalmus menestriesi Motschoulsky, 1862. Etudes entomol., Pt. XI, p. 41.

Type locality.—Mammoth Cave, Edmonson Co., Kentucky.

Range.—Caves of Edmonson, Barren and Hart Cos., Kentucky.

Pseudanophthalmus orlindae Barr
Pseudanophthalmus orlindae Barr, 1959. J. Tenn. Acad. Sci., 34:7.
Type locality.—Jesse James Cave, 1.5 miles southeast of Orlinda, Robertson Co., Tennessee.
Range.—Caves along the South Fork of Red River, Kentucky and Tennessee.

Pseudanophthalmus orthosulcatus Valentine
Pseudanophthalmus grandis orthosulcatus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:265.
Pseudanophthalmus orthosulcatus Valentine, Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:68.
Type locality.—Greenville, Saltpeter Cave, Monroe Co., West Virginia.
Range.—Type locality and Laurel Creek Caves, Monroe Co., West Virginia.

Pseudanophthalmus packardi Barr
Pseudanophthalmus packardi Barr, 1959. J. Tenn. Acad. Sci., 34:22.
Type locality.—Bat Cave, Carter Co., Kentucky.
Range.—Known only from type locality.

Pseudanophthalmus petrunkevitchi Valentine
Pseudanophthalmus petrunkevitchi Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:652.
Type locality.—Skyline Caverns, 2 miles southwest of Front Royal, Warren Co., Virginia.
Range.—Known only from type locality.

Pseudanophthalmus potomaca potomaca Valentine
Pseudanophthalmus potomaca Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:262.
Pseudanophthalmus hubbardi potomaca Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:651.
Pseudanophthalmus potomaca potomaca Valentine, Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:63.
Type locality.—Simmons Cave, Cave, Pendleton Co., West Virginia.
Range.—Type locality and Vandeventer's Cave, Highland Co., Virginia.

Pseudanophthalmus potomaca senecae Valentine
Pseudanophthalmus potomaca senecae Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:263.
Pseudanophthalmus hubbardi senecae, Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:351.
Pseudanophthalmus potomaca senecae Valentine, Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:64.
Type locality.—Seneca Caverns, Riverton, Pendleton Co., West Virginia.
Range.—Seneca Caverns, Nameless and Stratosphere Ballon caves, Pendleton Co., West Virginia.

Pseudanophthalmus pubescens Horn
Pseudanophthalmus pubescens Horn, 1868. Trans. Am. Entomol. Soc., 2:124.
Type locality.—Cave City Cave, Barren Co., Kentucky.
Range.—Caves in vicinity of Cave City, Barren Co., Kentucky.

Pseudanophthalmus punctatus Valentine
Pseudanophthalmus pusio var. punctatus Valentine, 1931. J. Elisha Mitchell Sci. Soc., 46:250.
Pseudanophthalmus punctatus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:266.
Type locality.—Tawney's Cave, Newport, Giles Co., Virginia.
Range.—Known only from type locality.

Pseudanophthalmus pusio pusio Horn
Pseudanophthalmus pusio Horn, 1868. Trans. Am. Entomol. Soc., 2:124.
Pseudanophthalmus pusio pusio Horn, Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:268.
Type locality.—Erhart's Cave, 5 miles east of Christianburg, Montgomery Co., Virginia.
Range.—Known only from type locality.

Pseudanophthalmus pusio bathycola Valentine
Pseudanophthalmus pusio bathycola Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:268.
Type locality.—Aunt Nellie's Cave, 3 miles southeast of Blacksburg, Montgomery Co., Virginia.
Range.—Known only from type locality.

Pseudanophthalmus robustus robustus Valentine
Pseudanophthalmus robustus robustus Valentine, 1931. J. Elisha Mitchell Sci. Soc., 46:250.
Type locality.—Johnson Cave, near Calfkiller, Putnam Co., Tennessee.
Range.—Caves of Putnam and northern White Cos., Tennessee.

Pseudanophthalmus robustus beaklei Valentine
Pseudanophthalmus robustus beaklei Valentine, 1937. J. Elisha Mitchell Sci. Soc., 53:97.
Type locality—Bunkum Cave, Byrdstown, Pickett Co., Tennessee.
Range—Caves of Pickett and Fentress Cos., Tennessee and southern Clinton and Wayne Cos., Kentucky.

Pseudanophthalmus robustus farrelli Barr
Pseudanophthalmus robustus farrelli Barr, 1959. J. Tenn. Acad. Sci., 34:12.
Type locality.—Indian Grave Point Cave, 6 miles southwest of Smithville, De Kalb Co., Tennessee.
Range.—Caves of southern De Kalb Co., Tennessee.

Pseudanophthalmus robustus lupus Barr
Pseudanophthalmus robustus lupus Barr, 1959. J. Tenn. Acad. Sci., 34:14.
Type locality.—Wolf River Cave, Fentress Co., Tennessee.
Range.—Known only from type locality.

Pseudanophthalmus robustus megosteus Barr
Pseudanophthalmus robustus megosteus Barr, 1959. J. Tenn. Acad. Sci., 34:12.
Type locality.—Big Bone Cave, Van Buren Co., Tennessee.
Range.—Caves of Van Buren Co., Tennessee.

Pseudanophthalmus robustus neglectus Jeannel
Pseudanophthalmus robustus neglectus Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:51.
Type locality.—Cumberland Caverns, Warren Co., Tennessee.
Range.—Caves of eastern Warren Co., Tennessee.

Pseudanophthalmus rotundatus Valentine
Pseudanophthalmus rotundatus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 27:271.
Type locality.—English Cave, 5 miles southwest of Cumberland Gap, Claiborne Co., Tennessee.
Range.—Type locality and Cooper's Cave, Hancock Co., Tennessee.

Pseudanophthalmus shilohensis shilohensis Krekeler
Pseudanophthalmus shilohensis Krekeler, 1958. Am. Midl. Nat., 59:178.
Pseudanophthalmus shilohensis shilohensis Krekeler, Barr, 1960. Am. Midl. Nat., 63:317.
Type locality.—Shiloh Church Cave, near Eureka Springs, Lawrence Co., Indiana.

Range.—Caves of western Lawrence Co., Indiana.

Pseudanophthalmus shilohensis boonensis Krekeler

Pseudanophthalmus boonensis Krekeler, 1958. Am. Midl. Nat., 59:180.

Pseudanophthalmus shilohensis boonensis Krekeler, Barr, 1960. Am. Midl. Nat., 63:318.

Type locality.—Boone Cave, 1 mile north of Freeman, Owen Co., Indiana.

Range.—Known only from type locality.

Pseudanophthalmus shilohensis mayfieldensis Krekeler

Pseudanophthalmus mayfieldensis Krekeler, 1958. Am. Midl. Nat., 59:178.

Pseudanophthalmus shilohensis mayfieldensis Krekeler, Barr, 1960. Am. Midl. Nat., 63:318.

Type locality.—Mayfield's Cave, 5 miles west-by-northwest of Bloomington, Monroe Co., Indiana.

Range.—Caves of central Monroe Co., Indiana.

Pseudanophthalmus striatus Motschoulsky

Pseudanophthalmus striatus Motschoulsky, 1862. Etudes entomol., Pt. XI, p. 41.

Type locality.—Mammoth Cave, Edmonson Co., Kentucky.

Range.—Caves of Edmonson, Barren and Hart Cos., Kentucky.

Pseudanophthalmus templetoni templetoni Valentine

Pseudanophthalmus templetoni Valentine, 1948. Geol. Surv. Alabama, Mus. Pap. no. 27:7.

Pseudanophthalmus templetoni templetoni Valentine, Barr, 1959. J. Tenn. Acad. Sci., 34:15.

Type locality.—Cumberland Caverns, Warren Co., Tennessee.

Range.—Caves of eastern Warren and northern Grundy Cos., Tennessee.

Pseudanophthalmus templetoni vanburenensis Barr

Pseudanophthalmus templetoni vanburenensis Barr, 1959. J. Tenn. Acad. Sci., 34:15.

Type locality.—McElroy Cave, Van Buren Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus tenesensis Valentine

Pseudanophthalmus tenesensis Valentine, 1937. J. Elisha Mitchell Sci. Soc., 53:98.

Type locality.—Grand Caverns, Byington, Knox Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus tenuis tenuis (Horn)

Anophthalmus tenuis Horn, 1871. Trans. Am. Entomol. Soc., 3:327.

Anophthalmus eremita Horn, Leng, 1920. Catalogue of Coleoptera, p. 55.

Pseudanophthalmus eremita Jeannel, 1928. L'Aveille, 32:131.

Pseudanophthalmus bloomi Krekeler, 1950. Am. Midl. Nat., 59:172.

Pseudanophthalmus tenuis tenuis (Horn) Barr, 1960. Am. Midl. Nat., 63:312.

Type locality.—Wyandotte Cave, Crawford Co., Indiana.

Range.—Caves of Crawford, Harrison and southern Washington Cos., Indiana.

Pseudanophthalmus tenuis blatchleyi Barr

Pseudanophthalmus tenuis blatchleyi Barr, 1960. Am. Midl. Nat., 63:312.

Type locality.—Truitt's Cave, near Bloomington, Monroe Co., Indiana.

Range.—Known only from type locality.

Pseudanophthalmus tenuis jeanneli Krekeler

Pseudanophthalmus jeanneli, Krekeler, 1958. Am. Midl. Nat., 59:171.

Pseudanophthalmus tenuis jeanneli Krekeler, Barr, 1960. Am. Midl. Nat., 63:315.

Type locality.—Elrod's Cave, 2 miles east of Orangeville, Orange Co., Indiana.

Range.—Known only from type locality.

Pseudanophthalmus tenuis morrisoni Jeannel

Pseudanophthalmus eremita morrisoni Jeannel, 1931. Arch. Zool. exp. Gen., 71:451.

Pseudanophthalmus morrisoni Krekeler, 1958. Am. Midl. Nat., 59:171.

Pseudanophthalmus tenuis morrisoni Jeannel, Barr, 1960. Am. Midl. Nat., 63:315.

Type locality.—Donaldson Cave, 4 miles east of Mitchell, Lawrence Co., Indiana.

Range.—Known only from type locality.

Pseudanophthalmus tenuis stricticollis Jeannel

Pseudanophthalmus eremita stricticollis Jeannel, 1931. Arch. Zool. Exp. et Gen., 71:468.

Pseudanophthalmus stricticollis Krekeler, 1958. Am. Midl. Nat., 59:170.

Pseudanophthalmus tenuis stricticollis Jeannel, Barr, 1960. Am. Midl. Nat., 63:315.

Type locality.—Marengo Cave, 12 miles north of Wyandotte Cave, Crawford Co., Indiana.

Range.—Known only from type locality.

Pseudanophthalmus tiresias tiresias Barr

Pseudanophthalmus tiresias tiresias Barr, 1950. J. Tenn. Acad. Sci. 34:16.

Type locality.—Indian Grave Point Cave, 6 miles southwest of Smithville, De Kalb Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus tiresias acherontis Barr

Pseudanophthalmus tiresias achernotis Barr, 1959. J. Tenn. Acad. Sci., 34:20.

Type locality.—Echo Cave, 2 miles northeast of Rockvale, Rutherford Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus tiresias bendermani Barr

Pseudanophthalmus tiresias bendermani Barr, 1959. J. Tenn. Acad. Sci., 34:21.

Type locality.—Benderman Cave, Southport, Maury Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus tiresias catherinae Barr

Pseudanophthalmus tiresias catherinae Barr, 1959. J. Tenn. Acad. Sci., 34:17.

Type locality.—Petty Cave, Marshall Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus tiresias insularis Barr

Pseudanophthalmus tiresias insularis Barr, 1959. J. Tenn. Acad. Sci., 34:18.

Type locality.—Baker Station Cave, northern Davidson Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus tiresias occidentalis Barr

Pseudanophthalmus tiresias occidentalis Barr, 1959. J. Tenn. Acad. Sci., 34:18.

Type locality.—DePriest Branch Cave, Lewis Co., Tennessee.

Range.—Caves of Cane Creek Valley, Lewis and Hickman Cos., Tennessee.

Pseudanophthalmus tiresias tullahoma Barr

Pseudanophthalmus tiresias tullahoma Barr, 1959. J. Tenn. Acad. Sci., 34:20.

Type locality.—Carroll Cave, Coffee Co., Tennessee.

Range.—Known only from type locality.

Pseudanophthalmus valentinei Jeannel
Pseudanophthalmus valentinei Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:51.
Type locality.—Johnson Cave, Putnam Co., Tennessee.
Range.—Caves of eastern Putnam and Overton Cos., Tennessee.

Pseudanophthalmus youngi youngi Krekeler
Pseudanophthalmus youngi Krekeler, 1958. Am. Midl. Nat., 59:175.
Pseudanophthalmus youngi youngi Krekeler, Barr, 1960. Am. Midl. Nat., 63:317.
Type locality.—Clifty Caves, 4 miles north of Campbellsburg, Washington Co., Indiana.
Range.—Known only from type locality.

Pseudanophthalmus youngi donaldsoni Krekeler
Pseudanophthalmus donaldsoni Krekeler, 1958. Am. Midl. Nat., 59:175.
Pseudanophthalmus youngi donaldsoni Krekeler, Barr, 1960. Am. Midl. Nat., 63:317.
Type locality.—Donaldson Cave, 4 miles east of Mitchell, Lawrence Co., Indiana.
Range.—Known only from type locality.

Catopidae

Ptomaphagus (Adelops) hirtus Tellkampf
Adelops hirtus Tellkampf, 1844. Müllers Archiv. Naturgesch., 10:33.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Caves of Edmonson, Barren and Hart Cos., Kentucky.

Ptomaphagus (Adelops) hatchi Jeannel
Ptomaphagus (Adelops) hatchi Jeannel, 1939. Bull. Soc. entomol. France, 1939:252.
Type locality.—Wonder Cave, Grundy Co., Tennessee.
Range.—Caves of southern Grundy and Franklin Cos., Tennessee.

Ptomaphagus (Adelops) henroti henroti Jeannel
Ptomaphagus (Adelops) henroti henroti Jeannel, 1949. Notes. Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:102.
Type locality.—Aladdin Cave, Sharp's Cove, Madison Co., Alabama.
Range.—Known only from type locality.

Ptomaphagus (Adelops) henroti ellipticus Jeannel
Ptomaphagus (Adelops) henroti ellipticus Jeannel, 1949. Notes. Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:102.
Type locality.—Shelta Cave, Huntsville, Madison Co., Alabama.
Range.—Shelta and Barclay Caves, Madison Co., Alabama.

Ptomaphagus (Adelops) hubrichti Barr
Ptomaphagus (Adelops) hubbrichti Barr, 1958. J. Tenn. Acad. Sci., 33:170.
Type locality.—Cripp's Mill Cave, 5 miles southwest of Smithville, DeKalb Co., Tennessee.
Range.—Caves of DeKalb Co., Tennessee.

Ptomaphagus (Adelops) laticornis Jeannel
Ptomaphagus (Adelops) laticornis Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:102.
Type locality.—Scott Cave, Sharp's Cove, Madison Co., Alabama.
Range.—Known only from type locality.

Ptomaphagus (Adelops) lodingi Hatch
Ptomaphagus (Adelops) lodingi Hatch, 1933. J. New York Entomol. Soc., 41:209.
Type locality.—Shelta Cave, Huntsville, Madison Co., Alabama.
Range.—Shelta and Barclay Caves, Madison Co., Alabama.

Ptomaphagus (Adelops) shapardi Sanderson

Ptomaphagus (Adelops) shapardi Sanderson, 1939. J. Kansas Ent. Soc., 12:121.

Type locality.—Dresser Cave, on Flore's Creek, near Fort Gibson Dam, Cherokee Co., Oklahoma.

Range.—Known only from type locality.

Ptomaphagus (Adelops) valentinei valentinei Jeannel

Ptomaphagus (Adelops) valentinei valentinei Jeannel, 1933. Bull. Soc. entomol. France, 1933:252.

Type locality.—Sauta Cave, Lim Rock, Jackson Co., Alabama.

Range.—Known only from type locality.

Ptomaphagus (Adelops) valentinei jonesi Jeannel

Ptomaphagus (Adelops) valentinei jonesi Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:103.

Type locality.—Pitts sinkhole, head of Big Cove, Madison Co., Alabama.

Range.—Known only from type locality.

Ptomaphagus (Adelops) valentinei longicornis Jeannel

Ptomaphagus (Adelops) valentinei longicornis Jeannel, 1949. Notes Biospeol. fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:103.

Type locality.—Cave Spring Cave, near Berkeley, Madison Co., Alabama.

Range.—Known only from type locality.

Pselaphidae

Arianops (Arispeleops) cavernensis Park

Arianops (Arispeleops) cavernensis Park, 1951. Geol. Surv. Alabama, Mus. Pap. no. 31:41.

Type locality.—Saltpeter Cave, Marshall Co., Alabama.

Range.—Known only from type locality.

Arianops (Arispeleops) jeanneli Park

Arianops (Arispeleops) cavernensis jeanneli Park, 1956. J. Tenn. Acad. Sci., 31:85.

Type locality.—Gilly's Cave, Pennington Gap, Lee Co., Virginia.

Range.—Known only from type locality.

Arianops (Arispeleops) stygica Park

Arianops (Arispeleops) stygica Park, 1960. Am. Midl. Nat., 64:67.

Type locality.—Cumberland Caverns, Warren Co., Tennessee.

Range.—Known only from type locality.

Batriasymmodes quisnamus (Park)

Batrisodes quisnamus Park, 1951. Geol. Surv. Alabama, Mus. Pap. no. 31:20.

Batrisodes jeanneli Park, 1951. Geol. Surv. Alabama, Mus. Pap. no. 31:21.

Batrisodes reduncus Park, 1956. J. Tenn. Acad. Sci., 31:65.

Batriasymmodes quisnamus (Park) Park, 1960. Am. Midl. Nat., 64:82.

Type locality.—Bunkum Cave, Byrdstown, Pickett Co., Tennessee.

Range.—Type locality; Pratt Cave, Pickett Co.; Lindsay Williams Cave, De Kalb Co.; Burial Cave, Jackson Co. and Sam Lackey Cave, Sumner Co., Tennessee.

Batriasymmodes spelaeus (Park)

Batrisodes spelaeus Park, 1951. Geol. Surv. Alabama, Mus. Pap. no. 31:16.

Batriasymmodes spelaeus (Park) Park, 1960. Am. Midl. Nat., 64:82.

Type locality.—Bangor Cave, Blount Co., Alabama.

Range.—Known only from type locality.

Batriasymmodes troglodytes (Park)

Batrisodes troglodytes Park, 1951. Geol. Surv. Alabama, Mus. Pap., no. 31:23.

Batriasymmodes troglodytes (Park) Park, 1960. Am. Midl. Nat., 64:82.
Type locality.—Rock Cave, Greenville, Butler Co., Alabama.
Range.—Known only from type locality.

Batrisodes (Babnormodes) barri Park
Batrisodes (Babnormodes) barri Park, 1958. J. Tenn. Acad. Sci., 33:40.
Type locality.—Dickson Cave, 1.5 miles south of Dickson, Dickson Co., Tennessee.
Range.—Dickson Cave and Columbia Caverns, Dickson Co., Tennessee.

Batrisodes (Babnormodes) clypeospecus Park
Batrisodes (Babnormodes) clypeospecus Park, 1960. Am. Midl. Nat., 64:71.
Type locality.—Reed Creek Cave, Fentress Co., Tennessee.
Range.—Type locality and Upper and Lower Parrot Caves, Overton Co., Tennessee.

Batrisodes (Babnormodes) ferulifer Park
Batrisodes (Babnormodes) ferulifer Park, 1960. Am. Midl. Nat., 64:69.
Type locality.—Benderman Cave, Southport, Maury Co., Tennessee.
Range.—Known only from type locality.

Batrisodes (Babnormodes) gemmoides Park
Batrisodes (Babnormodes) gemmoides Park, 1960. Am. Midl. Nat., 64:68.
Type locality.—Columbia Caverns, Dickson Co., Tennessee.
Range.—Known only from type locality.

Batrisodes (Babnormodes) gemmus Park
Batrisodes (Babnormodes) gemmus Park, 1956. J. Tenn. Acad. Sci., 31:71.
Type locality.—Jewel Cave, 12 miles northwest of Dickson, Dickson Co., Tennessee.
Range.—Known only from type locality.

Batrisodes (Babnormodes) henroti Park
Batrisodes (Babnormodes) henroti Park, 1956. J. Tenn. Acad. Sci., 31:70.
Type locality.—Vance Cave, Park City, Barren Co., Kentucky.
Range.—Vance and Beckton Caves, Barren Co.; caves of Edmonson and Hart Cos., Kentucky.

Batrisodes (Babnormodes) hubrichti Park
Batrisodes (Babnormodes) hubrichti Park, 1958. J. Tenn. Acad. Sci., 33:41.
Type locality.—Beckton Cave, 0.4 miles northwest of Beckton, Barren Co., Kentucky.
Range.—Known only from type locality.

Batrisodes (Babnormodes) jocuvestus Park
Batrisodes (Babnormodes) jocuvestus Park, 1960. Am. Midl. Nat., 64:70.
Type locality.—Aladdin Cave, Maysville, Sharp's Cove, Madison Co., Alabama.
Range.—Known only from type locality.

Batrisodes (Babnormodes) jonesi Park
Batrisodes (Babnormodes) jonesi Park, 1951. Geol. Surv. Alabama, Mus. Pap. no. 31:27.
Type locality.—Little Bear Cave, Tuscumbia, Colbert Co., Alabama.
Range.—Caves of western half of Colbert Co., Alabama.

Batrisodes (?Babnormodes) krekeleri Park
Batrisodes (?Babnormodes) krekeleri Park, 1960. Am. Midl. Nat., 64:74.
Type locality.—Cave Spring, 2.5 miles south-southwest of New Washington, Clark Co., Indiana.
Range.—Known only from type locality.

Batrisodes (Babnormodes) pannosus Park

Batrisodes (Babnormodes) pannosus Park, 1960. Am. Midl. Nat., 64:72.

Type locality.—Pedigo Cave, Cookeville, Putnam Co., Tennessee.

Range.—Known only from type locality.

Batrisodes (Babnormodes) profundus Park

Batrisodes (Babnormodes) profundus Park 1956. J. Tenn. Acad. Sci., 31:68.

Type locality.—Turk's (Brooklyn) Cave, near Brooklyn, Conecuh Co., Alabama.

Range.—Known only from type locality.

Batrisodes (?Babnormodes) schneiderensis Park

Batrisodes (?Babnormodes) schneiderensis Park, 1960. Am. Midl. Nat., 64:75.

Type locality.—Schneider Ranch Cave, 12 miles north-northeast of Boerne, Kendall Co., Texas.

Range.—Known only from type locality.

Batrisodes (Babnormodes) specus Park

Batrisodes (Babnormodes) specus Park, 1951. Geol. Surv. Alabama, Mus. Pap. no. 31:35.

Type locality.—Hutton Cave, Sharp's Cove, Madison Co., Alabama.

Range.—Caves of southern Tennessee and northern Alabama.

Batrisodes (Babnormodes) subterraneus Park

Batrisodes (Babnormodes) subterraneus Park, 1951. Geol. Surv. Alabama, Mus. Pap., no. 31:30.

Type locality.—Griffith Cave, Guntersville, Marshall Co., Alabama.

Range.—Known only from type locality.

Batrisodes (Babnormodes) tumoris Park

Batrisodes (Babnormodes) tumoris Park, 1960. Am. Midl. Nat., 64:73.

Type locality.—McClusky Cave, Colbert Co., Alabama.

Range.—Known only from type locality.

Batrisodes (Babnormodes) valentinei Park

Batrisodes (Babnormodes) valentinei Park, 1951. Geol. Surv. Alabama, Mus. Pap., no. 31:32.

Type locality.—Goat Cave, Keel Mountain, Madison Co., Alabama.

Range.—Caves of northern Alabama and southern Tennessee.

Batrisodes (Excavodes) cavernosus Park

Batrisodes (Excavodes) cavernosus Park, 1951. Geol. Surv. Alabama, Mus. Pap., no. 31:25.

Type locality.—Hinson Cave, Greenville, Butler Co., Alabama.

Range.—Known only from type locality.

Bythinopsis hubrichti Park

Bythinopsis hubrichti Park, 1960. Am. Midl. Nat., 64:76.

Type locality.—Copelin Cave, 2 miles east of Millerstown, Hart Co., Kentucky.

Range.—Known only from type locality.

Bythinopsis jonesi Park

Bythinopsis jonesi Park, 1951. Geol. Surv. Alabama, Mus. Pap., no. 31:43.

Type locality.—Wolf Den Cave, near Maud, Colbert Co., Alabama.

Range.—Known only from type locality.

Machaerites (Speleochus) croceus Park

Macherites (Speleochus) croceus Park, 1960. Am. Midl. Nat., 64:78.

Type locality.—Lott Cave, near Brownsboro, Madison Co., Alabama.

Range.—Lott and Twin Caves, Madison Co., Alabama.

Machaerites (Speleochus) stygius Park

Machaerites (Speleochus) stygius Park, 1951. Geol. Surv. Alabama, Mus. Pap., no. 31:47.

Type locality.—Toll Gate Natural Well, Monte Sano Mountain, Madison Co., Alabama.
Range.—Madison Co., Alabama.

Machaerites (Speleochus) synstygicus Park
Machaerites (Speleochus) synstygicus Park, 1956. J. Tenn. Acad. Sci., 31:64.
Type locality.—Barclay Cave, King Mountain, Madison Co., Alabama.
Range.—Known only from type locality.

Machaerites (Subterrochus) eurous Park
Machaerites (Subterrochus) eurous Park, 1960. Am. Midl. Nat., 64:79.
Type locality.—Jess Elliot Cave, Jackson Co., Alabama.
Range.—Known only from type locality.

Machaerites (Subterrochus) ferus Park
Machaerites (Subterrochus) ferus Park, 1951. Geol. Surv. Alabama, Mus. Pap., no. 31:49.
Type locality.—Aladdin Cave, Sharp's Cove, Madison Co., Alabama.
Range.—Madison and Jackson Cos., Alabama.

Machaerites (Subterrochus) steevesi Park
Machaerites (Subterrochus) steevesi Park, 1960. Am. Midl. Nat., 64:80.
Type locality.—Guffey Cave, Marshall Co., Alabama.
Range.—Known only from type locality.

Speleobama vana Park
Speleobama vana Park, 1951. Geol. Surv. Alabama, Mus. Pap., no. 31:53.
Type locality.—McClunney (Alabama) Caverns, near Clay, Jefferson Co., Alabama.
Range.—Known only from type locality.

ARACHNIDA

PHALANGIDA

Nemastomatidae

Nemastoma inops Packard
Nemastoma inops Packard, 1886. Am. Nat., 18:203.
Type locality.—Bat Cave, Carter Co., Kentucky.
Range.—Caves of northern Kentucky.

Nemastoma packardi Roewer
Nemastoma troglodytes Packard, 1877. Bull. U. S. Geol. Surv. Terr (Hayden), 3:160.
Nemastoma packardi Roewer, 1914. Arch. Naturg, 80:163.
Type locality.—Clinton's Cave, Lake Point, Tooele Co., Utah.
Range.—Known only from type locality.

Nemastoma pallidimaculosa Goodnight and Goodnight
Nemastoma pallidimaculosa Goodnight and Goodnight, 1945. J. New York Entomol. Soc., 53:241.
Type locality.—Rockhouse Cave, Oleander, Marshall Co., Texas.
Range.—Known only from type locality.

Phalangoididae

Phalangodes armata Tellkampf
Phalangodes armata Tellkampf, 1844. Archiv fur Naturgeschite, 10:320.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Caves of Kentucky and Tennessee.

Phalangodes californica (Banks)
Scotolemon californica Banks, 1900. J. New York Entomol. Soc., 8:200.
Phalangodes californica (Banks) Roewer, 1912. Archiv. Naturg. 78A:142.
Type locality.—Alabaster Cave, El Dorado Co., California.
Range.—Known only from type locality.

Texella mulaiki Goodnight and Goodnight
Texella mulaiki Goodnight and Goodnight, 1942. Am. Mus. Novitates, no. 1188:10.
Type locality.—San Marcos, Hays Co., Texas.
Range.—Known only from type locality.

Triaenonychidae
Sclerobonus cavicolens (Banks)
Cytobonus cavicolens Banks, 1905. Entomol. News, 16:251.
Sclerobonus cavicolens (Banks) Crosby and Bishop, 1924. Entomol. News, 35:109.
Type locality.—Morrison's Cave, 60 miles west of Bozeman, Madison Co., Montana.
Range.—Known only from type locality.

ARANEAE

Agelenidae
Cicurina buwata Chamberlin and Ivie
Circurina buwata Chamberlin and Ivie, 1940. Bull. Univ. Utah, Biol. Ser., 5(9):74.
Type locality.—Unnamed cave near Austin, Travis Co., Texas.
Range.—Known only from type locality.

Leptonetidae
Leptoneta coeca Chamberlin and Ivie
Leptoneta coeca Chamberlin and Ivie, 1942. Bull. Univ. Utah, Biol. Ser., 7:10.
Type locality.—Heidrich Cave, New Braunfels, Comal Co., Texas.
Range.—Known only from type locality.

Linyphiidae
Anthrobia monmouthia Tellkampf
Anthrobia monmouthia Tellkampf, 1844. Wiegman's Arch. f. Naturg., 10:318.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Virginia to Kentucky.
Phanetta subterranea (Emerton)
Linyphia subterranea Emerton, 1875. Am. Nat., 9:279.
Phanetta subterranea (Emerton) Keyserling, 1886. Spinnen Amerikas, Theridiidae, 2:125.
Type locality.—Wyandotte Caverns, Crawford Co., Indiana.
Range.—Caves of southeastern United States.
Willibaldia cavernicola Keyserling
Willibaldia cavernicola Keyserling, 1886. Spinnen Amerikas, Theridiidae, 2:123.
Type locality.—Reynold's Cave, Barren Co., Kentucky.
Range.—Caves of southeastern United States.

Nesticidae
Ivesia tennesseensis Petrunkevitch
Ivesia tennesseensis Petrunkevitch, 1925. Ann. Entomol. Soc. Am., 18:321.
Type locality.—Indian Cave, 5 miles northwest of New Market, Jefferson Co., Tennessee.
Range.—Caves of Kentucky, Tennessee and West Virginia.
Nesticus carteri Emerton
Nesticus carteri Emerton, 1875. Am. Nat., 9:279.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Caves of Kentucky and Tennessee.
Tuganobia potteria Chamberlin
Tuganobia potteria Chamberlin, 1933. Pan-Pac. Entomol., 9:124.

Type locality.—Potter Creek Cave, Shasta Co., California.
Range.—Known only from type locality.

Ochyroceratidae

Usofila gracilis Marx

Usofila gracilis Marx, 1891. Proc. Entomol. Soc. Wash., 2:35.
Type locality.—Alabaster Cave, El Dorado Co., California.
Range.—Caves of California.

ACARINA

Eupodidiae

Rhagida cavicola Banks

Rhagida cavicola Banks, 1897. Am. Nat., 31:382.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Known only from type locality.

Linopodes mammouthia Banks

Lonopodes mammouthia Banks, 1897. Am. Nat., 31:383.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky.
Range.—Known only from type locality.

MOLLUSCA

GASTROPODA

MESOGASTROPODA

Bulimidae

Amnicola aldrichi antroecetes Hubricht

Amnicola aldrichi antroecetes Hubricht, 1940. Nautilus, 53:120.
Type locality.—Shemmler's Cave, 2 miles south of Bluffside, St. Clair Co., Illinois
Range.—Cave streams of eastern Ozarks.

Amnicola procerpina Hubricht

Amnicola procerpina Hubricht, 1940. Nautilus, 53:121.
Type locality.—Rice's Cave, Jefferson Co., Missouri.
Range.—Type locality and a spring, Osage Hills Golf Course, Kirkwood, St. Louis Co., Missouri.

Horatia micra Pilsbry and Ferriss

Horatia micra Pilsbry and Ferriss, 1906. Proc. Acad. Nat. Sci. Phila., 58:112.
Type locality.—Drift on Guadalupe River, 4 miles above New Braunfels, Comal Co., Texas.
Range.—Southern Texas.

Carychiidae

Carychium stygium Call

Carychium stygium Call, 1897. Am. Nat., 31:387.
Type locality.—Mammoth Cave, Edmonson Co., Kentucky
Range.—Type locality, Buzzard's Cave and White's Cave, Edmonson Co., Kentucky.

CHORDATA

OSTEICHTHYES

TELEOSTEI

Amblyopsidae

Amblyopsis rosae (Eigenmann)

Typhlichthys rosae Eigenmann, 1898. Proc. Indiana Acad. Sci., 1897:231.
Ambylopsis rosae (Eigenmann) Woods and Inger, 1957. Am. Midl. Nat., 53:245.
Type locality.—Sarcoxie, Jasper Co., Missouri.
Range.—Southwestern corner of Missouri.

Amblyopsis spelea Dekay
Amblyopsis spelea Dekay, 1842. Zoology of New York or the New York Fauna, Part IV, Fishes, p. 187.
Type locality.—Mammoth Cave, Edmonson, Kentucky.
Range.—Limestone region of Indiana from Bedford south to Corydon and Edmonson Co., Kentucky.

Chologaster agassizi Putnam
Chologaster agassizi Putnam, 1872. Am. Nat., 6:22.
Type locality.—Lebanon, Wilson Co., Tennessee.
Range.—Caves and springs of the limestone region from southern Illinois to central Kentucky and north central Tennessee.

Typhlichthys subterraneus Girard
Typhlichthys subterraneus Girard, 1859. Proc. Acad. Nat. Sci. Phila., 1859:63.
Type locality.—Bowling Green, Warren Co., Kentucky.
Range.—Limestone region from southern Missouri to central Kentucky and Tennessee to northern Alabama.

Ictaluridae

Satan eurystomus Hubbs and Bailey
Satan eurystomus Hubbs and Bailey, 1947. Occ. Pap. Mus. Zool., Univ. Mich., 499:4.
Type locality.—A well, near San Antonio, Bexar Co., Texas.
Range.—Known only from type locality.

Trogloglanis pattersoni Eigenmann
Trogloglanis pattersoni Eigenmann, 1919. Proc. Am. Phil. Soc., 58:397.
Type locality.—A well near San Antonio, Bexar Co., Texas.
Range.—Artesian wells of San Antonio, Bexar Co., Texas.

AMPHIBIA

URODELA

Plethodontidae

Eurycea neotenes neotenes Bishop and Wright
Eurycea neotenes Bishop and Wright, 1937. Proc. Biol. Soc. Wash., 50:142.
Eurycea neotenes neotenes Bishop and Wright, Schmidt 1953. Checklist North American Amphibians and Reptiles, p. 55.
Type locality.—Culebra Creek, 5.0 miles north of Helotes, Bexar Co., Texas.
Range.—Bexar Co., Texas.

Eurycea neotenes latitans Smith and Potter
Eurycea neotenes Smith and Potter, 1946. Herpetologica, 3:107.
Eurycea neotenes latitans Smith and Potter, Schmidt 1953. Checklist North American Amphibians and Reptiles, p. 55.
Type locality.—Cascade Caverns, 4.6 miles southeast of Boerne, Kendall Co., Texas.
Range.—Known only from type locality.

Eurycea troglodytes Baker
Eurycea troglodytes Baker, 1957. Texas J. Sci., 9:328.
Type locality.—Valdina Farms sinkhole, Medina Co., Texas.
Range.—Known only from type locality.

Gyrinophilus lutescens (Rafinesque)
Triturus lutescens Rafinesque, 1832. Atlantic J., 1:121.
Gyrinophilus lutescens (Rafinesque) Mittleman, 1942. Proc. New Eng. Zool. Club, 20:33.
Type locality.—Eastern Kentucky.
Range.—Caves of northern Kentucky.

Gyrinophilus palleucus McCrady
Gyrinophilus palleucus McCrady, 1954. Copeia, 1954:29.
Type locality.—Sinking Cove Cave, Franklin Co., Tennessee.
Range.—Caves of Franklin Co., Tennessee.

Haideotriton wallacei Carr
Haideotriton wallacei Carr, 1939. Occ. Pap. Boston Soc. Nat. Hist., 8:335.
Type locality.—A well, Albany, Dougherty Co., Georgia.
Range.—Type locality and three caves in Jackson Co., Florida.

Typhlomolge rathbuni Stejneger
Typhlomolge rathbuni Stejneger, 1896. Proc. U. S. Nat. Mus., 18:620.
Type locality.—San Marcos, Hays Co., Texas.
Range.—Hays, Kendall and Comal Cos., Texas.

Typhlotriton spelaeus Stejneger
Typhlotriton spelaeus Stejneger, 1892. Proc. U. S. Nat. Mus., 15:116.
Type locality.—Rock House Cave, Barry Co., Missouri.
Range.—Ozark Plateau in Missouri and Arkansas and adjacent Kansas and Oklahoma.

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Adventive Plants New to the Missouri Flora

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During the summers of 1956-1958, the writer continued the collection of material for a comprehensive adventive flora of St. Louis (Mühlenbach, 1957). Again, a number of species not previously recorded for Missouri have been discovered. Thirty-three (omitting several not positively determined) are published in the following list. They were without exception, collected within the city limits of St. Louis. The writer wishes to express his appreciation for their assistance to Drs. F. J. Hermann, I. M. Johnston, J. Sauer, G. B. Van Schaack and J. A. Steyermark. Specimens verifying these records have been deposited in the herbarium of the Missouri Botanical Garden. The initials and numbers in parentheses below are those of the writer in field collections.

Aira elegans Willd.—This European grass is wide-spread, particularly in the states along the Atlantic and Pacific coasts. Hitchcock (1951:299) cites it from Missouri's neighboring states, Tennessee and Arkansas. A small colony was found on the levee of the Mississippi River, 100-200 m north of the Municipal Bridge, just opposite Crunden Martin Manufacturing Company's plant, May 13, 1956 (V. M. 614). The colony was destroyed the following year by the transformation of the whole territory into a municipal launching area for small boats.

Bromus squarrosus L.—This European grass is rare in the United States. Fernald (1950:103) reports it from Connecticut to Michigan, while Hitchcock (1951:50) mentions only Michigan, but adds North Dakota. There are recent collections in Indiana (Steyermark and Swink, 1955) and Montana (Booth and Wright, 1953). One well-developed specimen was found on the right-of-way of the Terminal Railroad, between the Signal-box Carrol Street Tower and Rutger Street, June 17, 1956 (V. M. 954).

Festuca myuros L.—This European grass according to Hitchcock (1951:63) is found in most coastal states, in Ohio, Wisconsin and Arizona; it is also reported from Oklahoma (Waterfall, 1951). It has now been found several times in St. Louis: 1) in the Lindenwood freight yard of the Frisco Railroad, at the eastern entrance of the yard, June 9, 1956 (V. M. 928); 2) a quite large colony in the center of the same yard, June 2, 1957, (V. M. 1194); 3) right-of-way of the Missouri-Pacific Railroad at the corner of Chouteau Avenue and Third Street, one specimen, June 17, 1956 (V. M. 949).

Puccinellia airoides (Nutt.) Wats. & Coult.—The range of this native western grass reaches its eastern limits in Wisconsin, Nevada

and Kansas and it is adventive in Vermont and Maine (Hitchcock, 1951:80). Therefore, it is not impossible that the specimens found in St. Louis could be native to Missouri. The collection data are: Carrie Avenue freight yard of the Terminal Railroad, only two specimens along the switch tracks in the northern part of the yard, June 1, 1957 (V. M. 1179). This freight yard is especially rich in adventive plants, so the native status of this grass, at least at this station, is dubious.

Paspalum dilatatum Poir.—A native of South America, it has been introduced into the United States since about the middle of the last century. According to Hitchcock (1951:615) it is now spread through all the southeastern states, as well as in some western ones. It is also known from all the states along Missouri's southern border. A few specimens were found directly on the border of the right-of-way of the Wabash Railroad and the parking lot of the Super Service Station, 3000 N. Broadway. Inquiry confirmed the supposition that trucks from southern states frequently use this lot for parking. For the great majority of adventive plants the railroads are responsible for their introduction; here one must think of the possibility that the seeds were brought by trucks. The next grass on the list also grows nearby and is a characteristically southern plant. The data of collection are: September 8, 1957 (V. M. 1355).

Paspalidium geminatum (Forsk). Stapf.—This grass of the warmer regions of both hemispheres, according to Hitchcock (1951:680) is known from Florida, Louisiana, Texas and Oklahoma. The data of collection are: June 30, 1957, September 8, 1957 (V. M. 1246 and 1354). Only a single specimen was found in the same locality where the previous mentioned grass *Paspalum dilatatum* was growing. Since the plant had developed a quite large clump, it was possible at both collections to remove pieces of the plant for the herbarium and still leave a part of it for further observation.

Lolium persicum Boiss. & Hohen.—In the United States this rye-grass is known only from North Dakota (Hitchcock, 1951:275), where it was possibly introduced from Russia. It was found in the Baden freight yard of the M.-K.-T. Railroad, north of the junction with tracks of the Terminal Railroad, four specimens, July 1, 1957 (V. M. 1214).

Hordeum jubatum L. var. *caespitosum* (Scribn.) Hitchcock.—This variety of a very common St. Louis species is a typical western one; the nearest states where it grows are North Dakota and Arizona (Hitchcock, 1951:268). Only four specimens were found along the main switch tracks in the Bremen Avenue freight yard of the Terminal Railroad, July 4, 1956 (V. M. 995).

Carex Douglasii Boott.—According to Gleason (1952:I, 305) this native western sedge reaches its eastern limit in Iowa. It has been observed in the Carrie Avenue freight yard of the Terminal Railroad since 1956 as a small colony. The data of collection are: May 8, 1955, June 24, 1956, June 1, 1957 and June 28, 1958, (V. M. 571,

971, 1178, 1424, respectively). The specimens seem to be male, most probably a single clone. It is quite astonishing that the plant withstood all destructive powers, especially the weed killers to which the whole vegetation of this part of the freight yard is regularly subjected each year.

Carex nebraskensis Dewey.—This American sedge is not mentioned by Fernald (1950) nor by Gleason (1952). The data of collection are: North St. Louis freight yard of the Burlington Railroad, along the 5th switch track counted from the east, June 15, 1957 (V. M. 1199). Dr. F. J. Hermann, who examined the specimen, expressed the opinion that its seeds could have been brought in on box cars. The nearest other record according to Hermann (1936) is northwestern Kansas.

Allium Cepa L. var. *viviparum* Metz.—Escapes of common cultivated plants are frequently overlooked and even if found, not considered worthy of reporting. So this plant, like a half dozen of other escapes in this list, has no previous record for Missouri. Only two specimens were found in an open spot between Davis Street Junction of the Missouri-Pacific Railroad, the grain elevator of the same company and Van Buren Street, May 30, 1957 (V. M. 1165). This place has been visited frequently since 1954, but the *Allium* was never observed before 1957. The manner of its introduction is difficult to determine. There are no kitchen gardens in the vicinity, nor is the place used for dumping.

Hemerocallis fulva L. var. *Kwanso* Regel.—Only one plant was found in the northeastern corner of the Carrie Avenue freight yard of the Rock Island Railroad, opposite the station, July 4, 1957 (V. M. 1257). Although there was not a trace of dumping in the near vicinity, some other escapes, such as *Miscanthus sinensis* Anderss., *Polygonum cuspidatum* Sieb. & Zucc., *Viola tricolor* L., *Cucurbita Pepo* L. grew nearby.

Rumex pulcher L.—This European dock, according to Fernald (1950:570) and Gleason (1952: II, 69) is now naturalized in a number of states, the nearest to Missouri being Arkansas and Oklahoma. This plant was found twice: 1) right-of-way of the Missouri-Pacific Railroad opposite its shed at First Street, corner Plum Street, one specimen, June 17, 1956 (V. M. 957); 2) two specimens on the right-of-way of Missouri-Pacific Railroad, opposite a shed at Second Street, corner Ashley Street, July 7, 1957 (V. M. 1261).

Celosia argentea L. var. *cristata* (L.) Ktze.—This plant is commonly cultivated. It was found here twice: 1) Baden freight yard of M.-K.-T. Railroad between the rails of a switch track south of the track scale, one juvenile specimen, September 1, 1957 (V. M. 1354); 2) right-of-way of the Missouri-Pacific Railroad, north of Dover Street, where the tracks enter the narrow space between the levee of the

Mississippi River and the steep and very high bluff, also one specimen, September 14, 1957 (V. M. 1364). There are some gardens on the top of the plateau over the bluff and so the seeds could come down from there, but the plant grew quite near to the rail, so its transport by train is also possible.

Amaranthus Powellii S. Wats.—According to Gleason (1952: II, 604) this western amaranth reaches its eastern limits in South Dakota, Oregon and West Texas and is adventive from Maine to Pennsylvania. In addition Jones and Fuller (1955: 194) mention Illinois. The data of collection are: 1) the right-of-way of the Terminal Railroad, between W. Florissant Avenue and Broadway, opposite the plant of Hussmann Refrigerator Company, one specimen, August 28, 1955 (V. M. 736); 2) Bremen Avenue freight yard of the Terminal Railroad, along the central switch tracks approximately opposite the engine house, scattered, July 4, 1958 (V. M. 1435).

Brassica napus L. ssp. *Napobrassica* L.—The data for the first record of Rutabaga as an escape in Missouri are: four specimens along the southern sidings of the grain elevator of the Missouri-Pacific Railroad, May 5, 1956 (V. M. 879).

Chorispora tenella (Willd.) DC.—This Asiatic plant is established in the northern states, Massachusetts to Iowa and Nebraska, and west to Washington (Fernald, 1950: 718). One specimen was found in the Lesperance Street freight yard of the Missouri-Pacific Railroad, along a switch track opposite to the gasometer, June 7, 1958 (V. M. 1412).

Phaseolus vulgaris L. var. *humile* Alef. For this commonly cultivated plant, there are no records for Missouri. A large colony was found in the Baden freight yard of the M.-K.-T. Railroad around the track scale of the yard, June 22, 1957 (V. M. 1228).

Anthriscus scandicina (Web.) Mansf.—This European plant is seldom found in the U. S. Fernald (1950: 1091) mentions only northeastern Virginia, but Gleason (1952: II, 619) adds the Pacific coast states. It is also reported from North Carolina (Ahles, Bell and Radford, 1958). It was found on a waste place between the Corneli Seed Company's building and Plum Street, near the Missouri-Pacific Railroad tracks on First Street; a few specimens, almost overgrown by other plants, May 13, 1956, June 17, 1956 (V. M. 887 and 960). It was found again the following year at the same place, but now forming a colony, May 25, 1957 (V. M. 1150).

Torilis nodosa (L.) Gaertn.—Gleason (1952: II, 614) reports this Mediterranean plant as abundant in the southern states, California and Oregon, and occasionally adventive in the range covered by Gleason's flora. Fernald (1950) does not mention the plant at all. A newer report is from North Carolina (Fox, Godfrey and Blomquist, 1950). In St. Louis it grew near the locality for *Paspalum dilatatum*

and *Paspalidium geminatum*, previously described in this list. A small colony, May 30, 1958 (V. M. 1403).

Apium graveolens L.—The data for the first record of this escape for Missouri are: sidings jointly owned by Frisco, Rock Island and Chicago and Eastern Illinois Railroads, east of the Federal Cold Storage building (1800 N. Broadway), north of Brooklyn Street, only two dwarf, not flowering, but easily recognizable specimens with the typical aromatic scent, September 7, 1957 (V. M. 1349).

Cuscuta indecora Choisy var. *neuropetala* (Engelm.) Hitchcock.—Fernald (1950: 1184) records the range of this parasitic plant to the south, to the west and partly to the north of Missouri; it also occurs to the east in Illinois. Therefore, there is a possibility that this plant could be native in Missouri. As in the case of *Puccinellia airoides*, one collection on a railroad territory cannot be considered decisive. The data of collection are: right-of-way of the Burlington Railroad, between East Grand Avenue and Ferry Street, along the sidings, June 30, 1956 (V. M. 973): a large colony, the hosts of the dodder being the very common (in St. Louis) *Convolvulus arvensis* L. and a completely dried crucifer probably *Erysimum repandum* L.

Aronnackia tenellata Gray.—This native western plant was collected four years ago, but determined only in 1958 by Dr. I. M. Johnston. The data of collection are: along the tracks of the Manufacturers Railway on DeKalb Street, south of President Street, a small colony, May 23, 1954 (V. M. 44). It has not been observed since 1954.

Galeopsis Tetrahit L.—This European plant is now a common weed in New England and in the southeastern and northern states (Fernald, 1950: 1228). Jones and Fuller (1955: 406) report it from Illinois. The data of collection are: 1) sidings of the local freight station of the Wabash Railroad (Third Street at Franklin Avenue), south of Carr Avenue, a single specimen, June 16, 1956 (V. M. 934); 2) Luther freight yard of the Wabash Railroad, by the side of a ramp in the northeastern corner of the yard, south of Humboldt Avenue, one specimen, June 30, 1956 (V. M. 978); 3) right-of-way of the Terminal Railroad, east of Sarah Avenue, again only one specimen, July 11, 1956 (V. M. 992). It is curious that all three widely separated specimens were discovered in one and the same year (1956); none was seen before or since, although this species is quite conspicuous so that it would be difficult to suppose that it was continually overlooked.

Ocimum basilicum L.—This tropical herb is infrequently cultivated in Missouri. Only one specimen was found on a recently established dumping ground along the Gimblin Road, just east of the Waterworks conduit track, where it was accompanied by many other garden escapes, September 1, 1957 (V. M. 1333).

Solanum villosum Mill.—Gleason (1952: III, 199) records this Eu-

rasian plant only along the Atlantic coast. Two specimens were found in the northeastern part of the Bremen Avenue freight yard of the Terminal Railroad along the central switch tracks, July 4, 1958 (V. M. 1436).

Antirrhinum majus L.—Again an escape, not previously reported from Missouri. The data of collection are: Carrie Avenue freight yard of the Rock Island Railroad, along the communication road running along the eastern border of the yard, approximately in the central part, a colony, August 25, 1956 (V. M. 1050). Here we have to deal not with an adventive plant, but a garden escape. The color of the corollas on various specimens differs considerably; some are greenish-yellow. The wild plants do not possess such a color; they are mostly red with a bright white tube, rarely white or pink with a yellow palate (Hegi, 1913:VI, 19). It is worth mentioning that dumping is quite frequent along the road.

Cosmos bipinnatus Cav.—This often cultivated, ornamental Central American plant escapes frequently from culture. The first escaped specimen in Missouri was found on the dump described above for *Ocimum basilicum* L., August 30, 1958 (V. M. 1471).

Artemisia vulgaris L.—Gleason (1952:III, 390) states that this European weed is now established throughout most of the eastern states. Fernald (1950:1522) cites, among other states, Michigan, Wisconsin and Minnesota; Jones and Fuller record it for Illinois (1955:465). One specimen was found in the Baden freight yard of the M.-K.-T. Railroad. It was badly damaged; the greater part of the stem was broken off and lay dried on the ground, August 30, 1958 (V. M. 1474).

Artemisia vulgaris L. var. *glabra* Ledeb.—Collection of this variety was made on the right-of-way of the Manufacturers Railway, north of Victor Street, opposite to the American Cone & Pretzel Company plant, along the fence of Vollmar Bros. Construction Company, a big colony, August 23 and October 5, 1958 (V. M. 1467 and 1495). At the time of a second visit the colony was destroyed with the exception of several individuals. Many dried stems lay around on the ground.

Senecio vulgaris L.—This native weed of the Old World is widely spread throughout most of the temperate zone (Gleason, 1952:III, 398). Only the Middle West seems to be an exception. There is no previous record for this plant from Missouri, but Jones and Fuller (1955:512) record it from Illinois. Again a single specimen was found, in the Carrie Avenue freight yard of the Terminal Railroad, June 28, 1957 (V. M. 1428).

Centaurea nigra L.—This European plant is now widely established according to Gleason (1952:III, 516) in the U.S. Fernald (1950:1544) cites several states, the nearest to Missouri being Ohio and

Michigan, but the plant occurs in Illinois also (Jones, 1947). It was found in the abandoned O'Fallon Street freight yard of the Terminal Railroad. When first discovered, there was but one plant, from which only fragments were taken. The data of collection are: June 16, 1956, July 14, 1956 (V. M. 941 and 1014). A small colony developed in the next year, one individual being at a distance from the original location, July 7, 1957 (V. M. 1262). But further spread of this plant did not occur. In the late autumn of 1957 all rails were pulled out and in 1958 the entire area (which harbored many other interesting and rare species) was paved and transformed into a parking lot for trucks.

Crepis pulchra L.—This European hawk's-beard is seldom met with in the United States. Gleason (1952:III, 528) gives the distribution as " . . . from Virginia, Ohio and Indiana and to be expected elsewhere." It was indeed found soon in North and South Carolina (Fox and Godfrey, 1949; Ahles, Bell and Radford, 1958). Now one can add Missouri too. One specimen was found in the Baden freight yard of the M.-K.-T. Railroad, west of the drinking fountain, July 5, 1958 (V. M. 1453).

Finally, several species are listed, the records for which were previously uncertain or incomplete.

Cyperus × *mesochorus* Geise. According to Dr. J. A. Steyermark (written communication) this is the first definite record from Missouri. The collection data are: 1) on the right-of-way of the Wabash Railroad south of the gravel plant at the foot of Branch Street, a colony, June 5, 1954 (V. M. 103); 2) on a waste place opposite to the Wabash Fruit Terminal, west of Collins Street, a huge clump, September 8, 1958 (V. M. 1485).

Carex Schweinitzii Dew.—This sedge is mentioned as native of Missouri in several floras, but according to Dr. J. A. Steyermark (written communication) he has seen this plant only from a St. Louis county record, preserved in the New York Botanical Garden Herbarium and identified by the late K. K. Mackenzie. No further information is given on the label. The first definite locations of this sedge are: 1) in the Carrie Avenue freight yard of the Rock Island Railroad, on a large free place south of Carrie Avenue, May 7, 1955 (V. M. 548); 2) in the Baden freight yard of the M.-K.-T. Railroad, west of the engine house, a colony in bushes, May 4, 1957 (V. M. 1136).

Boerhaavia erecta L.—Gleason (1952:II, 111) mentions that this southern plant extends as far north as Arkansas and possibly to Missouri. Dr. J. A. Steyermark writes me "reported before, but no specimen." One specimen in the Bremen Avenue freight yard of the Terminal Railroad, along the central switch tracks, west of the switch shanty, September 1, 1958 (V. M. 1481).

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On A New Genus of the Family Branchiobdellidae (Oligochaeta)

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As a result of current work devoted to the systematics of the Branchiobdellidae, it has become increasingly obvious that a satisfactory treatment of the family awaits the completion of detailed anatomical studies of the genera which compose it. The erection herein of a new genus, which includes the species formerly known as *Pterodrilus durbini* Ellis, is effected in order that an account of the anatomy of this species and a related form from Kentucky may be offered toward the completion of the task of understanding the evolutionary relationships of these interesting epizoans on decapods.

Moore (1895a), in a paper entitled "*Pterodrilus,* a remarkable discodrilid," established the genus *Pterodrilus* to receive the species *P. alicicornus* from the mountains of western North Carolina and *P. distichus* from western New York. The most obvious external features of these species are the dorsal bands and projections borne on the major annulations of certain body segments. Subsequently, Ellis (1918, 1919) recognized two other species of branchiobdellid worms with similar dorsal ridges or ridges and processes and assigned them to the genus *Pterodrilus.* He failed, however to give the detailed and accurate account of the reproductive system which Moore presented for his species. I have found that the internal anatomy of *P. durbini* is markedly at variance with that of the species Moore included in *Pterodrilus,* and this worm deserves, perhaps even more than *P. alcicornus* and *P. distichus,* to be described as "remarkable." The bursa is quite unlike that of the species of *Pterodrilus,* there is no spermatheca, and the clitellum is developed to an extent not equalled in any other known American branchiobdellid.

Since Ellis' original description of *P. durbini,* the only other reference to the species is Goodnight's (1940) statement that the single specimen examined by him agreed closely with Ellis' description. Goodnight said nothing as to the provenance of the specimen he saw.

The species does appear to be both localized and scarce. But during an extensive collecting trip in the summer of 1958, I was so fortunate as to take animals from Parke County, Indiana, which, on the basis of a direct comparison with Ellis's holotype of *P. durbini,* are conspecific with this type specimen. In addition, material of a related species was taken in central Kentucky.

This material has been studied both as whole mounts and serial sections. The animals were fixed in 4 percent formalin in 70 percent alcohol and preserved in 70 percent alcohol. Whole mounts were made by dehydrating, clearing and mounting unstained animals in balsam. Serial sections were prepared according to the usual methods

and stained in Delafield's hematoxylin and eosin. All drawings were made with the aid of a camera lucida, using the equipment and methods previously described (Holt and Hoffman, 1959). My catalog numbers for collections are indicated by the initials PCH.

Acknowledgment.—Financial support for my investigations of branchiobdellid systematics has been furnished by a grant (G-4439) from the National Science Foundation. In addition, I am grateful to Dr. Fenner A. Chace, Curator of Marine Invertebrates, United States National Museum, for permitting me to study the type material of *Pterodrilus durbini* and to Dr. Horton H. Hobbs, Jr., of the University of Virginia, for identifying the host crayfish.

Genus **Ellisodrilus**,[1] new genus

Pterodrilus, Ellis 1918 (in part); *Pterodrilus,* Ellis 1919 (in part); *Pterodrilus,* Goodnight, 1940 (in part).

Type species.—*Ellisodrilus clitellatus,* new species (here designated).

Diagnosis.—Small branchiobdellid worms belonging to the subfamily, Cambarincolinae Goodnight, 1940; with a prominent clitellum on segments VI and VII; with a muscular eversible bursa; penis non-eversible; prostate incompletely separated from the spermiducal gland; without a spermatheca; anterior nephridial ducts opening to the outside through a common pore on the dorsum of segment III; jaws anisomorphic, subhomodont, dental formula 5-4 in known species.

Ellisodrilus clitellatus, new species
(Figures 1-4)

Diagnosis.—Small worms slightly less than 1.5 mm in average length (preserved material); with a raised ridge on the dorsum of the major annulation of segment VIII, without such ridges on other segments; bursa expanded in the equatorial plane, with a prominent anterior lobe; spermiducal gland tapering ectally; prostate subequal in diameter to the spermiducal gland; prostatic bulb obscure, evident only in sections.

Type specimens.—Holotype, U.S.N.M. No. 29935; one paratype, U.S.N.M. No. 29936 and eighteen paratypes retained in my collections (PCH 827), from Adair County, Kentucky.

Distribution and specimens examined.—*Ellisodrilus clitellatus* has been taken from the following localities in Kentucky: Metcalfe County, 3.4 miles east of Edmonton on U.S. Highway 68, from *Orconectes juvenilis* (Hagen). V. F. Holt and P. C. Holt, July 28, 1958. Five specimens mounted entire (PCH 824); Adair County, 8.9 miles east of Columbia on Ky. Highway 80, from *Cambarus distans* Rhoades. *Type locality.* V. F. Holt and P. C. Holt, July 28, 1958. In addition to the types noted above eight serially sectioned specimens (PCH 827).

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[1] Named in honor of the late Professor Max M. Ellis, American student of the branchiobdellids and author of one of the included species.

Distribution and affinities.—Members of the genus *Ellisodrilus* are known from Michigan, Indiana and Kentucky. Although collections of branchiobdellids from these regions are not extensive, the rarity with which members of the genus appear in a series of collections taken by me in Indiana and Kentucky and their absence until now in records from Tennessee, Arkansas and Wisconsin, regions equally well represented in collections, lead to the conclusion that *Ellisodrilus* is a genus endemic to the northeastern part of the Mississippi Valley and the central Great Lakes drainage. The affinities of the genus seem to lie with the large and widespread genus *Cambarincola* and the related genus *Pterodrilus.* The presence in animals belonging to the genus *Ellisodrilus* of a common opening of the anterior nephridia, a prostate gland, an eversible bursa, and non-eversible penis allies it with the two genera mentioned. More remotely, *Ellisodrilus* may be related to *Ceratodrilus* (Holt, 1960) which differs among other respects from these genera in the eversible nature of the penis. If this hypothesis of generic relationships is confirmed, *Ellisodrilus* and *Pterodrilus* are specialized offshoots of a common cambarincolid stock. The geographic and ecological factors which might explain this diversification are at present quite unknown and speculation about Tertiary and post-Pleistocene conditions in the midcontinental region of North America is unwarranted in this connection.

Discussion.—*Ellisodrilus clitellatus* is a small worm (1.43 mm, average length; range 1.12-1.69 mm, Fig. 1). The head is about one-fifth of the total body length and subequal in diameter to that of segment I and the sucker. Segment VII is the largest segment in diameter with segment VI approaching it in size. The greater diameter of these segments is accounted for by the well-developed clitellum borne by them. The clitellum of branchiobdellids is not the well-developed and distinctive structure that it is in terrestrial oligochaetes, but the body wall of the last two genital segments (VI and VII) is always glandular. The glandular nature of these segments is not, however, usually apparent in material mounted entire. In the species of *Ellisodrilus* there is an obvious clitellum which accounts in large part for the distinctive appearance of the worms. The clitellum is absent on the ventral surface of segment VI, but it completely encircles segment VII. The other distinguishing feature of the external appearance of *E. clitellatus* is the raised ridge present on the dorsum of the major annulation of segment VIII. There have been frequent references to such ridges, and the projections they sometimes bear, not only in the genus *Pterodrilus,* which was originally described on the basis of such "appendages," but also in the genus *Cambarincola.* Ellis (1918, 1919) noted the presence of "raised major annulations" as one of the distinguishing characteristics of his species, *Cambarincola chirocephala.* The degree of contraction of the animals, which may vary with the nature of the killing and preserving fluids used, almost surely affects the degree to which the anterior annulations of the body segments are elevated over the posterior ones. None-

theless, the transverse ridge borne on segment VIII of *E. clitellatus* is real and is accounted for by the presence of supernumerary longitudinal muscles which are located dorsal to the regular ones of the body wall and insert on the anterior and posterior margins of the major (anterior) annulation (Fig. 7). These supernumerary muscles are absent in the other segments of the body and the contraction of the longitudinal muscles consequent on fixation produces a generally smooth body outline (Fig. 1).

The jaws of *E. clitellatus* are anisomorphic, subhomodont, i. e., the teeth or denticles they bear are of approximately equal size, and the dental formula is 5-4 (Fig. 4). There is little, if anything, to distinguish them from those of *E. durbini* as described by Ellis (1919).

It is difficult to determine the position of the opening or openings of the anterior nephridia in whole mounts. Those of *E. clitellatus* open through a common pore on the dorsum of segment III.

The male reproductive system of the genus *Ellisodrilus* is distinctive. No attempt was made to measure or figure the male funnels, efferent or deferent ducts. They are all quite small in diameter, in keeping with the small size of the worms. The funnels are cylindrical in shape. The spermiducal gland (see Holt, 1960, for the nomenclature applied to the organs of the branchiobdellid reproductive systems) lies longitudinally in the coelom of segment VI, its dorsal border reaching almost, if not quite, to the dorsal border of the coelom. The gland tapers appreciably ectad as it approaches its junction with the ejaculatory duct (Fig. 2). The ental points of entry of the vasa deferentia into the gland lie close together and are not readily apparent in whole mounts.

Associated with the spermiducal gland is the structure Ellis called the "accessory sperm tube" which is referred to here as the "prostate." In the genus *Cambarincola* this structure, which ends blindly entally, empties into the ejaculatory duct in common with the spermiducal gland. In species of *Pterodrilus* (Moore, 1895a) it is incompletely separated from the spermiducal gland and in those of *Ceratodrilus* (Holt, 1960) it is reduced to a prostatic bulb on the side of the spermiducal gland. In *E. clitellatus* the prostate is incompletely separated from the spermiducal gland as in *Pterodrilus,* but it differs from the species of the latter genus in possessing a prostatic bulb, although this modification consisting of flattened epithelial cells at the blind ental end of the prostate is only readily seen in sections. The prostate of *E. clitellatus* differs from that of *E. durbini* as described below in being for the course of its distinctness as a lobe of the spermiducal gland approximately equal in diameter to the latter (Figs. 2 and 6). In some species of *Cambarincola* (Holt, 1949; Hoffman, in ms.) the prostate is composed of glandular cells which lack visible secretory granules and hence are different in appearance from those of the spermiducal gland. In the species of *Ellisodrilus* the prostate is composed of cells similar to those of the spermiducal gland as far as can be ascertained.

The ejaculatory duct of *E. clitellatus* resembles in structure that of other branchiobdellids (Holt, 1949). It courses along the posterior dorsal surface of the bursa and then turns mesad to enter the bursa at its posterior mesial border. There is really no differentiated penis present, the ejaculatory duct simply passes through the wall of the bursa and ends as a pore on the inner surface of the latter.

The bursa is one of the two remarkable features of the reproductive system. Basically it is a modification of the type of bursa found in the genus *Cambarincola* (Holt, 1949). The atrial or ectal part differs only in being elongated in the axis of the bursa (Fig. 3). The elongation of the atrium is produced by the unusually great development of the inwardly projecting circular fold of the bursal wall, the inner margin of which forms the rim of the cup-like everted bursa in the species of *Cambarincola* and *Pterodrilus,* which likewise have an eversible bursa and a non-eversible penis. The portion of the bursa which would form the penial sheath in other branchiobdellids is in *E. clitellatus* greatly expanded and produced into sac-like muscular lobes (Figs. 2 and 3) and there is, as noted above, no true penis. The everted bursa of *E. clitellatus* has not been seen, but it probably appears as a widely flaring and ruffled cup-shaped structure with a balloon-like projection within the "cup" composed of the ental expanded part and carrying at its outer — in the everted condition — border the opening of the ejaculatory duct.

The second really remarkable feature of the reproductive systems of *Ellisodrilus* is the complete absence of a spermatheca. Segment V, the normal location of the spermatheca, contains the usual amount of spermatogenic tissue and a pair of male funnels and efferent ducts and nothing else in the way of reproductive structures. No means of fertilization has been observed and the functioning of the elaborate structure of the male apparatus would seem to involve some form of "hypodermic" impregnation. But no evidences of this have been observed and speculation in the present state of knowledge of these worms is futile.

Ellisodrilus durbini (Ellis)
(Figures 5-7)

Pterodrilus durbini, Ellis, 1918; *Pterodrilus durbini,* Ellis, 1919; *Pterodrilus durbini,* Goodnight, 1940.

Diagnosis.—Small worms, slightly more than 1.5 mm in average length (preserved material); with raised ridges on the major annulations of segments II, III, IV, V, VII, and VIII; bursa expanded but anterior lobe not as prominent as in *E. clitellatus;* spermiducal gland cylindrical throughout its length; diameter of prostate approximately one-half that of the spermiducal gland; prostatic bulb often obscure in whole mounts.

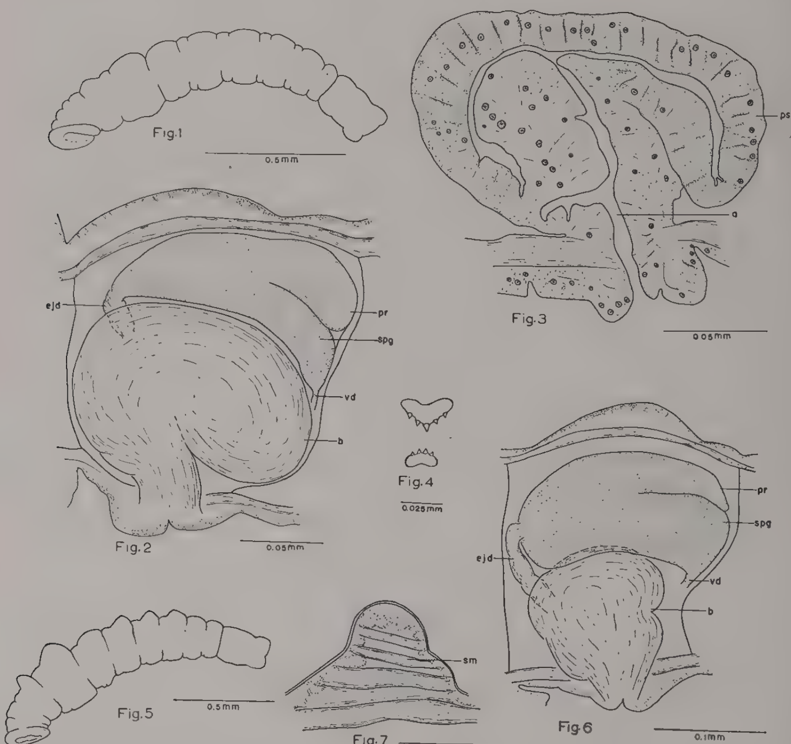
Type specimens.—Holotype and two paratypes, U.S.N.M. No. 17655, Madison County, Indiana.

Distribution and specimens examined.—*E. durbini* is known from

Indiana and Michigan. I have examined materials from the following localities in Indiana: Madison County, White River at Irondale near Anderson, from *Cambarus rusticus* Girard. *Type locality.* Max M. Ellis, August, 1916. Holotype and two paratypes, U.S.N.M. No. 17655. Parke County, 4.2 miles north of Rockville on U.S. Highway 41, from *Orconectes propinquus propinquus* (Girard). V. F. Holt and P. C. Holt, July 26, 1958. Five specimens mounted entire (PCH 806).

In addition to the above cited records, Ellis (1918) reported *E. durbini* from *Cambarus virilis* Hagen at seven localities in the vicinity of Potagannissing Bay, Michigan.

Discussion.—The name *durbini* for a species of branchiobdellid



Figs. 1-4. *Ellisodrilus clitellatus*, n. sp. 1. Outline drawing of type specimen. 2. Lateral view, male reproductive system. 3. Diagrammatic sketch of section through bursa. 4. Sketch of jaws. Figs. 5-7.—*Ellisodrilus durbini* (Ellis). 5. Outline drawing. 6. Lateral view, male reproductive system. 7. Longitudinal section through dorsal ridge of segment VIII. Abbreviations: *a*, atrium of bursa; *b*, bursa; *ejd*, ejaculatory duct; *pr*, prostate; *ps*, penial sheath; *sm*, supernumerary muscle fiber; *spg*, spermiducal gland; *vd*, vas deferens.

dates from 1918 when Ellis included it in a key to the branchiobdellids of northern Michigan and assigned the species to the genus *Pterodrilus.* Since this key consists of a list of diagnostic characters, the name *durbini* used in it would seem to constitute a valid proposal of a species name. But Ellis obviously intended that his paper published in 1919, which had been submitted for publication prior to the writing of the 1918 one, should have priority, and this paper contains the formal description of *durbini* and designates the type specimen.

Ellis made his generic assignment of the species on the basis of the raised ridges which characterize it. These ridges are found in species of several genera of branchiobdellids and can no longer be considered diagnostic of the genus *Pterodrilus.* Their nature has been discussed above. Ellis' species *durbini* clearly belongs with *Ellisodrilus clitellatus* and the absence of a spermatheca, along with other characters, in these species is certainly of generic importance.

One or two discrepancies between Ellis' (1919) description and the holotype designated by him, discrepancies which apply also to the animals from Parke County, Indiana, must be considered. Ellis stated that *durbini* possesses a tubular spermatheca. There is, however, no spermatheca in the animals designated as types! The only possible explanation is that this statement is based on the confusion of worms of another species from the same collection as the types of *durbini* with the latter. Such errors made by Ellis, and perhaps other earlier workers on the branchiobdellids, are due to the invalid assumption that a general correspondence in external appearance indicates a correspondence in internal structure and the failure to realize that one collection may include representatives of several species of worms.

Of less importance is the statement (Ellis, 1919) that there is a raised ridge on segment VI of *durbini.* This ridge is absent in the specimens from Parke County, Indiana. The types are strongly contracted and stained with carmine. The clitellum of segment VI of these specimens is indeed raised and it is impossible, due to the staining, to determine whether segment VI of the types has the supernumery muscles which produce a true raised ridge. It is assumed here that the raised appearance of segment VI in the types is accounted for by contraction of the animals and the clitellum. Of similar import are Ellis' statements concerning the "funnel-like" nature of the ridges on segments VII and VIII of his animals. This appearance of the types is produced by the clitellum in the contracted state of these animals. The two "horns" on the elevation of segment VIII of the types which Ellis mentioned, cannot be detected either in the types or any of the other animals examined.

E. durbini appears to be a somewhat larger animal than *E. clitellatus,* eight specimens of the former, including the types, average 1.64 mm in length (range 1.34-1.85 mm). The bodily proportions of the two species are similar and externally they differ only in the pre-

viously noted presence of ridges on the dorsa of other segments than VIII in *E. durbini* (Fig. 5).

Except for the differences in external anatomy and in the spermiducal gland, prostate and bursa discussed above, the two species are quite similar and no obvious differences were noted.

SUMMARY

The genus *Ellisodrilus* is defined and its affinities discussed.

A new species, *Ellisodrilus clitellatus* Holt, is diagnosed and designated the generotype.

Ellisodrilus durbini (Ellis) is removed from the genus *Pterodrilus* and the two species are compared.

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Electromigration Properties of Mammalian Hemoglobins as Taxonomic Criteria

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Introduction

In recent years many investigators have become interested in the comparative aspects of electromigration properties of specific animal proteins, and while many different proteins have been studied from this aspect, more work has been done on plasma proteins and hemoglobins than on all the others combined. Undoubtedly these two types have enjoyed this popularity because of the ease with which they may be obtained and purified. Since the plasma proteins may be affected by many environmental factors such as diet, temperature, and disease, the hemoglobins are probably better suited, from the standpoint of reproducibility, for comparative studies.

Several workers (Cabannes and Serain, 1955; Rodnan and Ebaugh, 1957; and Saha *et al.* 1957) have shown that within the vertebrate classes the hemoglobins of many species may differ from each other in electrophoretic mobility and in the number of separable hemoglobin components. However, the animals chosen by these workers were usually those available from domestic stocks and taxonomic relationships were so remote that little could be inferred concerning a possible correlation between phylogeny and hemoglobin types. Dessauer *et al.* (1957), on the other hand, have compared, within the Reptilia and Amphibia, animals of distant and close taxonomic kinships and have found consistent correlations between hemoglobin electrophoretic properties and phylogeny. These latter authors, while they suggested further study by other investigators, presented data showing that species within a genus and sometimes races within a single species might be distinguished by definite, though slight, differences in hemoglobin mobilities. Species more distantly related showed greater differences; however, the correlation between these differences and phylogeny, these authors state, is not sufficiently systematic to permit one to assign an animal to the proper category above the level of genus on the basis of hemoglobin ionograms alone.

It was felt that a similar study of mammals might prove equally enlightening. Since the author (1954) had previously investigated the hemoglobin-oxygen affinity of rodents, and since these are the most readily available wild mammals, the rodents were selected as the principal subjects for this investigation. Thus, in one study it should be possible to determine whether or not there are systematic relations among oxygen affinities, electromigration properties, and taxonomic kinships of specific hemoglobins.

I wish to express to the National Science Foundation my appreciation for the funds provided for the pursuit of this study.

MATERIALS

The following species were employed in this investigation.

CARNIVORA	
Bobcat (B)	*Lynx rufus*
LAGOMORPHA	
Eastern Cottontail (A)	*Sylvilagus floridanus*
RODENTIA	
SCIURIDAE	
Eastern Chipmunk (D)	*Tamias striatus*
Gray Squirrel (A)	*Sciurus carolinensis*
Red Squirrel (C)	*Tamiasciurus hudsonicus*
Flying Squirrel (C)	*Glaucomys volans*
ZAPODIDAE	
Jumping Mouse (C)	*Napaeozapus insignis*
MURIDAE	
Norway Rat (A)	*Rattus norvegicus*
House Mouse (A)	*Mus musculus*
CRICETIDAE	
Red-backed Mouse (C)	*Clethrionomys gapperi*
Meadow Vole (A, D)	*Microtus pennsylvanicus*
Muskrat (A)	*Ondatra zibethicus*
Golden Hamster	*Mesocricetus auratus*
Rice Rat (E)	*Oryzomys palustris*
Cotton Rat (A, E)	*Sigmodon hispidus*
Harvest Mouse (A, E)	*Reithrodontomys humulis*
Golden Mouse (A, C, E)	*Peromyscus nuttalli*
Cotton Mouse (E)	*Peromyscus gossypinus*
White-footed Mouse (A, C, D)	*Peromyscus leucopus*
Deer Mouse (C)	*Peromyscus maniculatus*
Oldfield Mouse (E)	*Peromyscus polionotus*

The above classification and scientific names, except *Mesocricetus*, are from Hall and Kelson (1959), and each individual has been carefully identified with the aid of descriptions and distribution maps from this work. Several questionable identifications were confirmed by comparison with known specimens in the Mammal Collection of the Department Zoology of North Carolina State College. No attempt was made to identify subspecies; however, the letters following the vernacular names indicate the sites of collection according to the following code: A—Stanly County, North Carolina; B—Montgomery County, North Carolina; C—Macon County, North Carolina; D—Lackawanna County, Pennsylvania; E—Colquitt County, Georgia.

METHODS

Blood samples were drawn by heart puncture from lightly etherized mammals with a 2 cc syringe and a 20 ga needle using heparin as an anticoagulant. From 0.5 to 2 cc of blood was then added to 7 cc of

isotonic saline in a centrifuge tube, was shaken thoroughly, and was centrifuged. The supernatent was discarded by aspiration, and this washing was repeated three times to remove all plasma constituents. The packed red cells, after washing, were lysed with two volumes of distilled water. The resulting hemoglobin solution was centrifuged at high speed for 30 minutes before being applied to paper strips for electrophoresis. For most species some hemoglobin solutions were shaken for five minutes with .5 volumes of toluene before the final centrifugation, as recommended by Drabkin (1946). This extraction with toluene made very little difference in the ionograms, and mobilities were more reproducible when this step was omitted. In view of this fact, and since several hemoglobins (especially those of the cotton rat and flying squirrel, tended to precipitate upon shaking with toluene, the mobilities in Figure 1 were measured from ionograms obtained from hemoglobin solutions without toluene extraction.

All ionograms were obtained from a Spinco Model R series D, Durrum-type paper electrophoresis cell, using a Heath Company PS-4 as a source of constant voltage. For all species standard ionograms were obtained using a barbital buffer at pH 8.6, ionic strength .0225 in a 15 percent glycerol solution with Schleicher and Schuell 2043A mgl paper strips. A constant voltage of 10 volts/cm was maintained for 8.0 hours at room temperature (20-27°C). Under these standard conditions the total distance that the hemoglobins moved on the paper strips was very nearly a linear function of time. This standard was chosen when it offered the greatest reliability after many trial runs with other voltages and various buffers at different pH. For most species additional ionograms were obtained at pH 9.2 with other conditions similar to those of the standard ionograms. For a few species ionograms were obtained using a borate buffer at pH 9.0. These additional ionograms were run in compliance with a suggestion by Itano (1957) that some hemoglobins might appear to be electrophoretically homogeneous under one set of conditions, while in other buffers of different pH they might be resolved into separable components. However, no significant differences were noted between standard and other ionograms obtained from the same hemoglobin solutions.

All ionograms were dried immediately for 30 minutes at 120-130°C and were finally stained with bromphenol blue dye and scanned with a Photovolt electronic densitometer, Model 525. From the scannings the mobility of each separate peak was measured and relative mobilities were established by comparison with human hemoglobin A under identical conditions.

Most hemoglobin solutions were run in duplicates which were usually not measurably different in mobility; nevertheless, occasional duplicates on adjacent strips would differ by as much as 10 percent. This would suggest a maximum experimental error in relative mobilities of about ± 5 percent when all controllable parameters were kept constant within the standard conditions. The relative mobilities

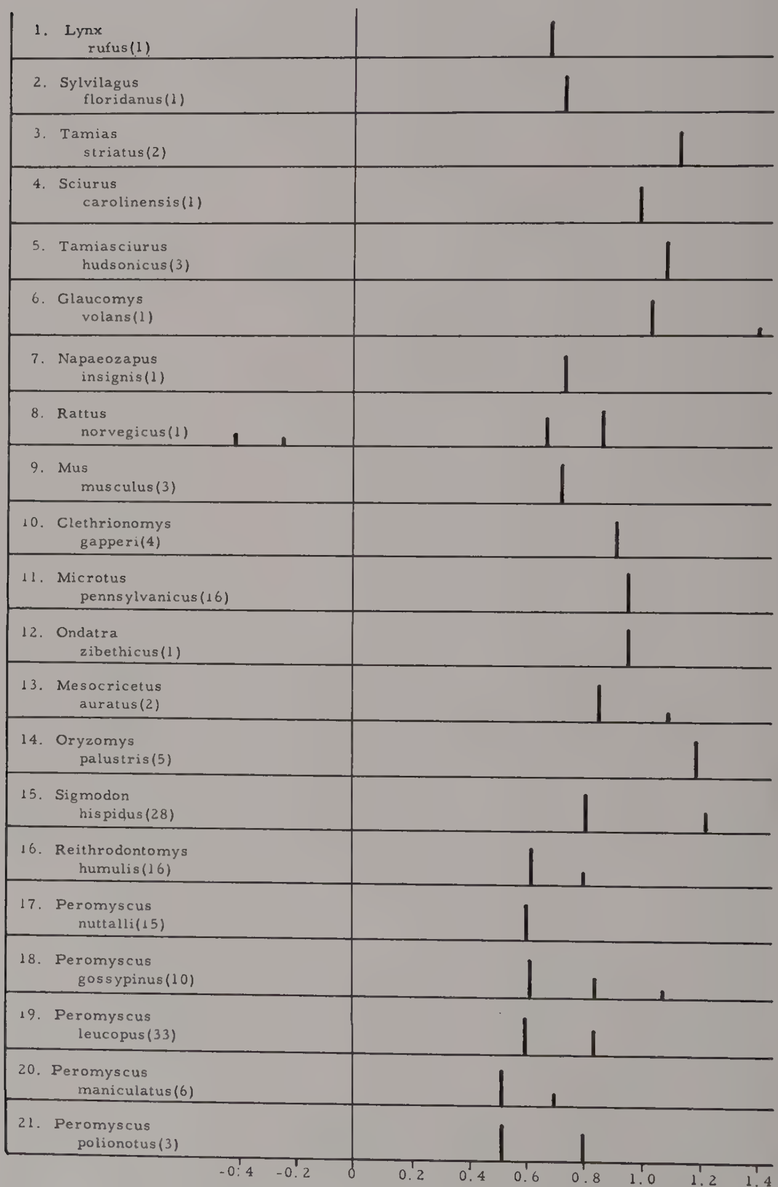

Fig. 1.—Graphic representation of typical hemoglobin ionograms. See text

reported here are probably somewhat different from those that might be obtained from moving boundary electrophoresis or from zone electrophoresis where other supporting media were employed. The reader is referred to McDonald (1955) for a discussion of mobility determinations in stabilized media.

RESULTS

Figure 1 summarizes the principal findings of this study. In this graph the distance from the origin may be read directly as the relative mobility; thus human hemoglobin A occupies the position 1.0. The numbers in parentheses indicate the number of individuals showing typical hemoglobin for each species. For those species with more than one hemoglobin the heights of the bars are constructed to indicate the relative proportions of each separable component as estimated from the scanning patterns described above. These proportions are only approximate, for they do not represent area measurements under absorption curves; instead, the proportions were obtained by measuring the heights of absorption peaks for each separable component. With these measurements as a guide, the height of the absorption peak for the major component was arbitrarily plotted on the graph to equal one; the heights of other components were then plotted to scale according to the ratio of the height of their absorption peak to that of the major component. Due to the high tendency of paper strips to adsorb hemoglobins and to the consequent excessive streaming, area measurements are impractical — especially when two components are not completely separated.

It may be readily noted that nearly half the species examined showed multiple hemoglobins, and that these, with the exception of the Norway rat, show a major component preceded by one or more minor components of higher mobility. This latter relationship is reversed in the Norway rat, and only the Norway rat and cotton mouse were found to possess more than two electrophoretically separable hemoglobins. Furthermore, only the Norway rat shows hemoglobins that migrate toward the cathode.

The mammals in Figure 1 are arranged so that members of taxonomic groups are together, and certain systematic relationships are thereby made more obvious. Thus, the similarities of the hemoglobins of the five species of *Peromyscus* are readily apparent. The major components of the hemoglobins of *P. leucopus, P. gossypinus,* and *P. nuttalli* seem to have the same relative mobility; however, the three specific hemoglobins are readily distinguishable, for they are characterized by one, two, and no minor components respectively. The major hemoglobin components of *P. maniculatus* and *P. polionotus* show almost identical relative mobilities which are slightly less than those of corresponding components of the other species of this genus; however, the difference lies within the range of experimental error and may not be significant. It should be noted that *Reithrodontomys*

humulus hemoglobins resemble those of *Peromyscus*. One other relationship stands out: all three members examined of the subfamily *Microtinae* (*Ondatra zebethicus, Microtus pennsylvanicus,* and *Clethrionomys gapperi*) show single hemoglobins of almost identical mobility. Similarities of electromigration properties, to be sure, do not necessarily reflect similarities of molecular structure nor of phylogenetic kinship, for the hemoglobins of the bobcat and house mouse are barely distinguishable when such properties are considered alone.

The hemoglobin patterns shown in Figure 1 are those most frequently found for the indicated species, and for 18 of the 21 species examined there were no measurable departures from these patterns. This fact is remarkable, for five species (see the list of subjects above) were represented by individuals collected from trapping stations separated by hundreds of miles. For three species, cotton mouse (*Peromyscus gossypinus*), white-footed mouse (*Peromyscus leucopus*), and cotton rat (*Sigmodon hispidus*), aberrant individuals were found with hemoglobin ionograms quite different from the typical ones presented in Figure 1. These three species must be considered individually.

Absorption curves were obtained by transmission scanning of hemoglobin ionograms of normal human hemoglobin and typical and aberrant cotton rats, cotton mice, and white-footed mice (Fig. 2). That for cotton mouse No. 105 is like the ten typical ones diagrammed in Figure 1. One additional cotton mouse, No. 83, is aberrant in that the middle hemoglobin component is lacking and the faster minor component occurs in several times the typical concentration. At this writing the latter mouse is still alive and has been checked three times to determine whether or not his aberrant pattern may change. So far, no change has been detected. An attempt is being made to breed him to a typical cotton mouse and to explore the genetics of this aberration.

Out of 18 white-footed mice from Lackawanna County, Pennsylvania, one, No. 159, presented the unusual pattern shown in Figure 2; the other 17 presented hemoglobin ionograms indistinguishable from those of 14 taken in Stanly County, North Carolina, and two more from Macon County, North Carolina. White-footed mouse, No. 160, in Figure 2 shows the typical absorption curve for this species with a major component and one slightly faster minor component. White-footed mouse, No. 159, is clearly aberrant by having the proportions between these two components almost exactly reversed. Unfortunately, this mouse died before any other data could be obtained.

From the standpoint of aberrant individuals, the cotton rat is most interesting. The typical pattern presented for this species in Figure 1 and for cotton rat No. 181 in Figure 2 was shown by 21 rats from Stanly County, North Carolina, and by 7 from Colquitt County, Georgia. In addition to these typical ones, two were taken in Stanly County with hemoglobin ionograms like that of cotton rat No. 150

in Figure 2, and two more similar ones were caught in Colquitt County. Only in Colquitt County, Georgia, where two were collected, were cotton rats like No. 149 in Figure 2 taken. Breeding experiments have been started with these aberrant animals, and the offspring obtained so far indicate that these hemoglobin electromigration patterns are genetically determined, probably by a single pair of genes; however, more data are needed to confirm this hypothesis. These breeding experiments will be continued.

In Figure 2 the small peaks at the origins are probably the results of small amounts of cellular debris that was not removed during the final centrifugation. When the hemoglobin solutions were shaken with toluene prior to centrifugation, these peaks at the origin failed to show. They are, therefore, thought to be of no significance.

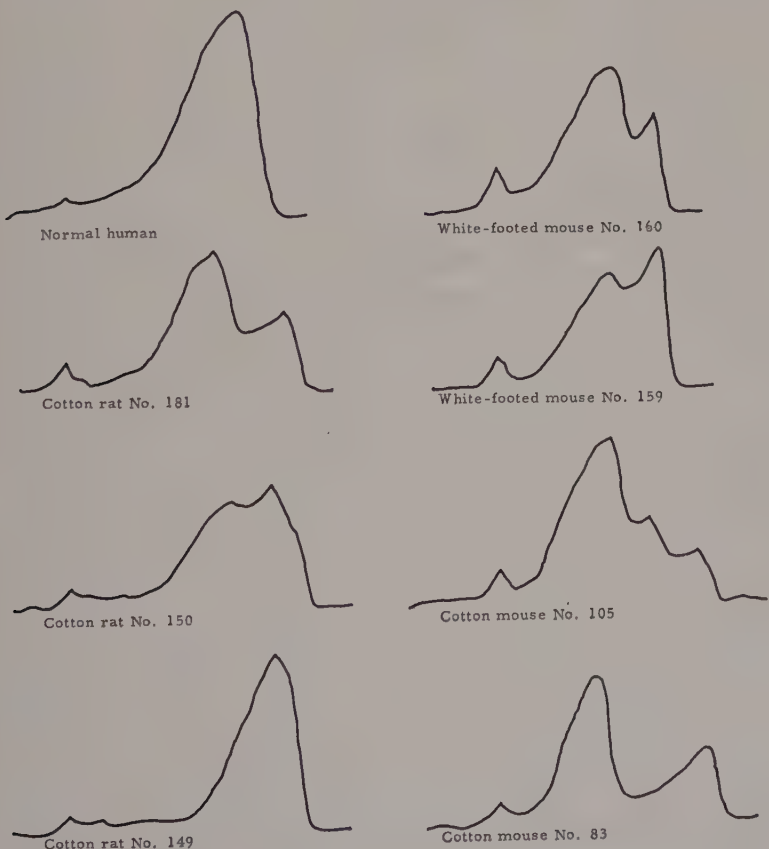

Fig. 2.—Scanning curves obtained by transmission densitometry of hemoglobin ionograms. See text

DISCUSSION

The data recorded in Figure 1 suggest that very closely related species may show certain similarities in the electromigration properties of their hemoglobins. Such similarities are clearly demonstrated in the genus *Peromyscus*. *P. nuttalli, P. leucopus,* and *P. gossypinus* seem to share a slow major component and differ from each other in the numbers of minor components. The slightly lower relative mobilities of the major components of *P. maniculatus* and *P. polionotus,* if real, are particularly noteworthy, for Dice (1940) reported that, in spite of their considerable morphological differences, these species interbreed freely in the laboratory and produce fertile offspring. Dice also reported a similar relationship between *P. leucopus* and *P. gossypinus,* even though these latter species remain intact in areas where both may be found. Dice was unable to obtain crosses between these two groups; e. g., *P. leucopus* will not cross with *P. maniculatus.* Similarities of electromigration properties may possibly extend to the hemoglobins of closely related genera, for *Reithrodontomys humulis* shows a hemoglobin ionogram very similar to that of *P. leucopus,* and representatives of the three genera in the subfamily *Microtinae* (mammals 10 through 12, Fig. 1) are almost indistinguishable in this regard. On the other hand, within the subfamily *Cricetinae* (mammals 14 through 21, Fig. 1) there is as much variation of ionogram type as there is between members of different orders. That *P. nuttalli* is the only species of *Peromyscus* examined which does not show more than one hemoglobin is relevant to Hooper's (1958) recent proposal that this species be elevated to a separate genus, *Ochrotomys.*

It is proposed that intrageneric differences of hemoglobin electromigration properties may serve as useful taxonomic criteria in the identification of morphologically similar species. Such use might be made of this criterion where the species *P. leucopus* and *P. gossypinus* have overlapping distributions. Even as adults these species may be distinguished in certain areas only by small quantitative differences in morphology, and the young of these species are almost identical. However, the young may be separated quite readily when their hemoglobin ionograms are compared. It must be pointed out that electromigration properties, as amply demonstrated by the cotton rat, may show individual departures from type and, therefore, offer no unique advantages. Like other taxonomic criteria, hemoglobin ionograms must be considered in combination with other characteristics and must be evaluated by persons with experience in each local situation.

That so many species with multiple hemoglobins should show major components with lower mobilities than the minor components is remarkable, for Buhler and Shanks (1959) report that the reverse is generally true in fishes. No physiological advantages nor disadvantages are known to be associated with these multiple hemoglobins.

Breeding experiments in progress here suggest that the deviations

cited above for certain individual cotton rats are the results of different combinations of a single pair of genes. The same is probably true for the deviant cotton mouse and white-footed mouse, for Gluecksohn-Waelsch *et al.* (1957), Russell and Gerald (1958), and Welling and Bekkum (1958) have shown somewhat similar deviations to be determined by single gene pairs in the laboratory mouse. If all the deviations reported here are the result of mutant genes, the loci concerned with hemoglobin production in rodents must be highly mutable. The frequency and distribution of these aberrations in wild populations certainly deserves further study.

The electromigration properties of specific hemoglobins reported here have been carefully compared with the hemoglobin-oxygen affinities established previously by the author (1954) for nine of the same species. There seems to be no correlation between oxygen affinities of specific hemoglobins and their electrophoretic mobilities.

SUMMARY

Results are presented of electrophoretic analyses of the hemoglobins of 161 individuals representing 21 species of mammals chosen carefully so that distantly related species might be compared with closely related ones. The following conclusions are demonstrated and discussed.

Individuals of the same species may, with few exceptions, exhibit characteristic hemoglobin ionograms that do not vary appreciably even though these individuals are taken from collecting stations separated by hundreds of miles.

Closely related species usually show striking similarities of hemoglobin electrophoretic patterns while distantly related species may or may not show such similarities.

Since it is shown that member species of a single genus may often be readily distinguished by definite, though slight, differences between the electromigration properties of their hemoglobins, it is proposed that hemoglobin ionograms may sometimes serve as useful taxonomic criteria with which to identify species that are morphologically very similar.

Somewhat rarely certain individuals may show hemoglobin ionograms that are markedly atypical for their species.

By comparing the hemoglobin ionograms of nine of the above species with the oxygen dissociation curves that the author had previously established, it was concluded that no correlation exists between hemoglobin electromigration properties and oxygen affinity.

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A Seven-Year Study of Cone Production as Related to Xylem Layers and Temperature in Pinus ponderosa

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In 1955 the writer published the results of a study of the thickness of xylem layers in *Pinus ponderosa* and three other tree taxa, all of which were sampled near their upper and lower limits of altitudinal distribution in eastern Washington and northern Idaho. No correlation with either temperature or precipitation, or their combined influence on the environmental water balance, could be found at either distributional extreme. One possible explanation is that whereas temperature and/or moisture might well set altitudinal limits through their control over *seedling success,* climate would not necessarily exert a critical control over *xylem production.* That is, the prevailing wetness of the soils at the start of summer might carry the plants along until the time of endogenous cessation of cambial activity in midsummer (Daubenmire, 1946; Daubenmire and Deters, 1947), but seedlings become increasingly vulnerable to drought throughout summer. Another possibility is that variations in fruiting habits of the trees might make periodically heavy demands on metabolites which could obscure weather influences in large measure. This paper presents the results of a study aimed primarily at determining what influence, if any, variations in cone production may have on the annual xylem increments of *Pinus ponderosa* in the same region as the first study mentioned.

Literature Review

Abundant fruiting, which commonly is not an annual event in the life of even a vigorous tree, tends to channel metabolites into the enlarging fruits. This is often reflected in reduced xylem production of the current season, and is sometimes carried over in part into the following summer.

Pyrus malus is notorious for its propensity for bearing fruit only on alternate years. Cambial growth is normally limited on the crop years (Overholser *et al.,* 1941, Singh, 1948; Wilcox, 1937) although McMunn (1939) found that a tree must bear more than 20 bushels of apples to show a narrowed xylem layer for that year. In northern New Brunswick nearly all *Abies balsamea* trees also exhibit this tendency for biennial bearing, and cone crops are associated with both narrower xylem layers and markedly shortened needles (Morris, 1951).

Many studies of *Fagus sylvatica* have shown that little xylem is laid down on heavy fruit years (Huber and Jazewitsch, 1956). Holmsgaard (1956) states that this influence is clear only after the trees reach an age of 100 years, and the effects, greatest in the upper part of the stem, persist for at least two succeeding years. Since the effect of fruiting may outweigh weather influences, he recommends using only trees

that have not yet reached reproductive age for establishing relations between weather and xylem deposition.

Picea abies likewise produces thinner wood layers in those seasons when heavy cone crops are maturing (Hoeg, 1956; Mikola, 1950; Eklund, 1954, 1957). Holmsgaard (1956) thinks that in *Picea* as well as in *Fagus* the exhaustive influence of fruiting may be felt for several years. Xylem increment is likewise negatively correlated with fruit production in *Prunus persica,* but there appears to be no hold-over effect in the following year (Proebsting, 1958).

The relations among climate, fruiting vigor and diameter increase are complicated in *Pinus* by the fact that cones grow during two summers before they ripen. In northern Finland *Pinus sylvestris* flowers heavily following a year of above-average diameter growth, with diameter growth being depressed in the flowering year (Hustich, 1948, 1956). But the relation is weakened by the fact that xylem production is also influenced by the weather of the preceding year, with a strong tendency for correlation between the widths of two subsequent years (Hustich, 1945; Eklund, 1954, 1956). Growth in pine is further complicated by the fact that it holds its needles for only a few years, therefore depends more heavily than *Picea* on the amount of foliage it has produced the preceding year. In the Rocky Mountains squirrel cutting of twigs of *Pinus ponderosa* introduces still another complication in that these twigs not only fall with next year's cones, but damage is greatest when the cone crop is small and it reduces the photosynthetic capacity of the tree subsequent to the small crop (Adams, 1955).

An endogenous rhythm seems operative in *Pyrus malus* and *Abies balsamea,* but among most other trees abundant fruiting seems the result of chance combinations and sequences of weather conditions, which have different effects on species with different ecologic requirements or tolerances. As a consequence of all the superimposed variables operating throughout the extended sexual cycle of *Pinus, P. ponderosa* in western North America produces good cone crops at intervals of 1-8 years in California (Fowells and Schubert, 1956) and 1-6 years in western Montana (Boe, 1954). Since weather at any one time in the reproductive cycle may nullify or enhance the effects of weather at another time, and since animal influences could easily obscure the effects of a metabolic shift from vegetative to reproductive physiology, one might anticipate difficulties in correlating cone crops with width of the annual wood increments. Inappropriate sampling may also have a bearing on investigations of the relations between growth layers and fruiting. There are some reports (Jaccard, 1915; Holmsgaard, 1955) that heavy seed production reduces the xylem increment chiefly within the canopy, so that the effect may be feeble at the height where trees are usually sampled for analyzing growth layers.

METHODS

In the NW/4 of Section 25, Township 15N, Range 43E, in Whitman County, Washington, there occurs a pure stand of *Pinus ponder-*

osa on the north-facing slope of a ravine. The stand is on the *Pinus ponderosa/Symphoricarpos rivularis* habitat type as defined by Daubenmire (1952) and rate of height growth is relatively high for eastern Washington, even though this particular site is below the average elevation of lower timberline, and forest is confined to the moist sides of the valleys.

By standing on the open ridgetop one can look into the tops of the pines and easily count their cone crops with field glasses in early September. In 1951 four trees having cones were numbered, and their cones counted. Also four trees in the same size range but lacking or almost lacking cones were tagged. Each succeeding year the cone crops were counted until the spring of 1958 when the stand was heavily culled and the record brought to an abrupt end. All cones visible from the one side were counted alternately by two observers[1] until a clearly defined modal value was established. It is estimated that perhaps 10 percent of the actual crop was not visible, but no correction factor has been applied to the data.

When logging began 3 increment cores were obtained from equally spaced radii from each tree at breast height, so that the thickness of the xylem layers could be measured and compared with the corresponding annual cone crops. The cores were dried, glued in grooved boards, sanded, and the layers measured under a binocular microscope.

Eight trees too young to have borne cones were also sampled and the xylem studied in identical manner.

RESULTS

Table I shows that although the trees had reached a very satisfactory height for their age (judged against an abundance of unpublished data gathered by the writer), cone production was erratic and, in general, perhaps less abundant than might be expected.

In Table II each cone crop was considered independently and all have been arranged in a sequence, ignoring totals less than 28. Whenever cone crops equalled 30/tree, less wood was laid down during the fruiting year in comparison with the flowering year. However, the significance of this relation is jeopardized when percent decrease is taken into account, for on a physiologic basis, the greater the expenditure of metabolites in fruit growth the greater should be the percentage reduction in diameter growth, but the data do not reflect such a proportionality. Furthermore, 7/8 of the young sterile trees also produced less wood in 1954 than in 1953. In other words, factors other than fruiting (probably weather) can account for practically all the reduction in cambial activity concomitant with heavy bearing in 1954. Overlapping influences of one cone crop on another that follows closely does not seem to be a complicating factor, for when trees 1 and 3 are removed from consideration because they bore at least moderately in both 1951 and 1954, there is no improvement in correlations among the other data. Comparisons of xylem formation between the

[1] I am indebted to Jean B. Dubenmire for assistance in this respect.

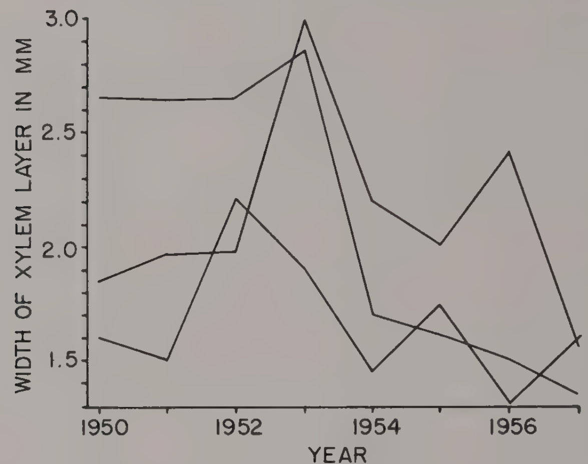

Fig. 1.—Annual variations in width of xylem layers along three radii at breast height. Data are from tree number six in Table I.

flowering year and the preceding year, as well as between the fruiting year and the subsequent year, have been omitted from Table II because relationships were erratic. Percentage summer wood (rather than total annual increment) studied in precisely the same manner likewise yielded no positive correlations.

The conclusion seems inescapable that cone production among these eight trees, over seven years of observation, cannot be correlated with thickness of the annual xylem increment of the preceding, current or subsequent years.

In the study alluded to in the introductory remarks in which the writer sought correlations between cambial growth and climate, the conclusion was reached that "so much discordance was found in the

TABLE I.—Tree dimensions as of March, 1955, and counts of freshly opened cones

Tree No.	Height in m	D.B.H. in cm	No. Xylem layers	Number of cones 1951	1952	1953	1954	1955	1956	1957
1	27.7	56	70	95	55	76	134	4	6	37
2	27.4	52	69	0	24	32	123	0	0	0
3	17.7	42	67	28	30	3	72	0	0	1
4	24.7	46	74	2	0	14	146	0	0	0
5	28.0	51	68	113	44	19	86	0	0	0
6	24.3	44	66	2	6	14	384	0	4	0
7	20.4	37	66	28	1	1	3	0	0	0
8	22.2	39	68	0	0	0	100	0	0	0
Total Cone Crop				268	160	159	1048	4	10	38

sequences of thick and thin layers along opposed radii of the same individual that no relationship between xylem formation and climate could be detected over a 50-year period" (Daubenmire, 1955). Apparently this erratic cambial behavior within an individual tree also obscures any possible correlation between xylem formation and fruiting vigor. Figure 1 shows the extent to which xylem thickness may vary on three radii of the same tree. The largely negative results of this study are parallel to those of Dow (1951) who found no correlation between cone production and rate of growth in *Larix laricina*.

CORRELATION BETWEEN WEATHER AND THE SEXUAL CYCLE

The successful maturation of a large crop of cones is made possible by a concatenation of favorable weather starting at some time prior to the laying down of flower initials. Each stage of the process, which involves about 27 months in *Pinus*, must be favored by weather conditions falling within the range required for that particular stage. A short stretch of unfavorable weather could easily nullify optimal conditions that may have prevailed up to that time.

It has long been known that summers with above-average temperature are conducive to the formation of an abundance of flower buds. By empirical methods it was discovered by the writer that by using mean monthly air temperatures and algebraically summing the monthly deviations from long-time means, the period June through September seems highly critical for laying down flower initials in the pine stand studied. In Table III cone crops are arranged in order of magnitude considering all 8 trees as a group, and it is clear that cone crops depend on above-average temperatures, with the size of the crop being closely related to the degree of deviation. Maguire (1956)

TABLE II.—Changes in mean width of xylem layers in mm during the reproductive cycle

Tree	Year	No. of cones	Width of Xylem, mm Flowering year	Fruiting year	Percent decrease
7	'51	28	1.72	1.93	0
3	51	28	1.77	1.96	0
3	52	30	1.96	1.60	18
2	53	32	2.78	2.37	15
1	57	37	1.83	1.46	20
5	52	44	2.72	2.55	6
3	54	72	1.81	1.29	29
5	54	86	2.94	1.89	36
1	51	96	2.99	2.79	7
8	54	100	1.68	1.40	17
5	51	113	2.92	2.72	7
2	54	123	2.37	2.15	9
1	54	134	2.67	2.21	17
4	54	146	.94	.54	43
6	54	384	2.58	1.78	31

TABLE III.—Temperature data (U. S. Weather Bureau records for Pullman, Wash.) in relation to abundance of cones

Year of cone ripening	Total cones on 8 trees	Temperature Conditions (°F) of pre-flowering year (ripening year minus two) Sums of means for Apr. + May*	Sums of deviations from means, Jun. thru Sept.
1954	1048	105.8	5.6
1951	268	108.3	3.6
1952	160	95.4	2.7
1953	159	102.5	2.9
1957	38	89.4	–5.9
1956	10	96.7	–17.4
1955	4	97.5	–2.3

* Long-time mean is 100.5°F.

found that summed mean temperatures for the two months April and May, are fairly well correlated with abundant formation of flower initials of *Pinus ponderosa* in California. This mode of expressing warmth of the induction period has no value for the ecotype studied in eastern Washington (Table III).

Since the correlation described above shows that, for the trees and years studied, the heat of the summer preceding flowering accounts for practically all variations in size of cone crop, it may be concluded that all subsequent combinations and sequences of temperature as well as other climatic variables were favorable to the reproductive processes. No further inquiry into weather controls seems warranted for these data.

SUMMARY

A seven-year record was kept of cones matured by eight trees of *Pinus ponderosa* growing on a highly productive habitat in eastern Washington. The thickness of wood layers along three equally spaced radii at breast height was so extremely variable for any one tree that no correlation could be established between wood deposition of the individual trees and their fruiting vigor.

Cone production is closely and positively correlated with the degree to which summer temperatures (June through September) are above-average for the year when flower initials are laid down.

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Biology of the Oligochaete Bimastos zeteki Smith and Gittins (Lumbricidae) in Northern Michigan

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General use of the term "earthworm" has tended to obscure very real differences in life histories of terrestrial Oligochaeta. As a result, ecologists have had inadequate information on these organisms with which to interpret the soil fauna. The problem, as a matter of fact, is not unique to the ecological viewpoint; with regard to morphology, Smith has written (1924):

> The common earthworm is a variety which is very frequently met with in more recent text-books, but not in collections. As described in a new textbook which appeared within the last year this variety would seem to be a hybrid form from ancestors belonging to two different genera of outdoor species and which also has acquired some additional characters found in none of them.

Direct analyses of earthworm populations, more often than not concerned with agricultural soils, have been largely quantitative, emphasizing population density as related to various edaphic factors. In this vein, a significant body of data has been made available through the various publications of Evans (1947; 1948), Guild (1948 through 1957), Evans and Guild (1947; 1948), Waters (1955), and Satchell (1955). In nearly every case, these authors and others, including Wilcke (1954), Julin (1949), Siivonen (1941), Boyd (1957), Bodenheimer (1935), and Bornebusch (1930), have underlined the risk involved in generalization; a risk of some magnitude when environmental factors are considered. As an example, we find Bodenheimer stating (1935):

> The conclusions of Arrhenius on the importance of soil acidity seems to be justified, but not so his generalization. It is obvious, that there exists no optimal pH for "the" earthworm, simply because no "average earthworm" exists, but a large number of different species of earthworms, each of which has its own optimum and its own range of tolerance toward the soil reactions of its environment.

The research reported here has been concerned quite specifically with the earthworm *Bimastos zeteki* Smith and Gittins (1915) as found in Michigan soils. Field work was accomplished over a period of three summers (1955-1957) largely in the area surrounding the University of Michigan Biological Station, Cheboygan County, Michigan. The main objectives of the work were to determine: (1) periodicity of *B. zeteki;* (2) habitat selection and use; (3) vital coefficients (deposition of oöthecae, growth rate, etc.) in field populations; and (4) the responses of *zeteki* to environmental stresses such as temperature and moisture changes.

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ation of my needs, and to Professor Irving Cantrall for making available the facilities of the E. S. George Reserve. My special thanks to Professors F. E. Eggleston and F. H. Test of the University of Michigan for their encouragement and advice. A portion of this work was accomplished during the tenure of a Faculty Research Fellowship, awarded the writer by the Horace H. Rackham School of Graduate Studies of the University of Michigan, for which I am deeply grateful.

MATERIALS

Bimastos zeteki is considered endemic to North America, its known range extending from Louisiana (Harman, 1952) to northern Michigan in the Midwest (Smith and Gittins, 1915; Murchie, 1956) and from Connecticut southward into North Carolina (Gates, 1956). Additional records are those of Causey (1952) from Arkansas, Olson (1928) from Ohio, and Smith (1917) for Illinois and Indiana. The species has invariably been reported as an inhabitant of decaying logs, leafy accumulations, and the soil immediately below such material. Virtual restriction of *zeteki* to woodlands and its absence from soils marginal to aquatic areas might suggest an inherent inability to compete with so-called peregrine earthworms (Smith, 1928). Murchie (1956) and Gates (1958) have pointed out that such restriction may be due to habitat selection related to changing land use or forest practice. Such alterations might permit invasion of an area by one species while creating barriers for another. No clear evidence of competition between earthworm species has ever been presented insofar as I am aware.

Seasonal activities of *Bimastos zeteki* have not heretofore received significant attention. Gates (1956) concluded, on the basis of morphological evidence, that the breeding season "would seem to include April in Connecticut, June in Virginia, July in the mountains of Tennessee and North Carolina." He further cites Heimburger (1915) for the observation that Indiana worms of this species were at the height of sexual activity in June.

The genus *Bimastos* has become a "taxonomic wastebasket" (Gates, 1956) but *zeteki* is unquestionably a "good" species and sexually mature individuals in Michigan collections conform to published descriptions (Smith and Gittins, 1915; Smith, 1917; Gates, 1956). Adult worms measure up to 150 mm in length and five mm in width at the clitellum. Their body color varies from pale red to chestnut brown. Usually, *Bimastos zeteki* shows a localized whitish banding caused by internal accumulation of yellowish-white corpuscles. Anteriorly the bands may occupy three segments, from III to V; posteriorly, about five sub-terminal segments may be involved. Except for the very small individuals recently emerged from oöthecae, no particular difficulty was experienced in identifying *zeteki* in the field.

AREA OF FIELD STUDY

Although most of the research was accomplished in Cheboygan County, Michigan, additional information was drawn from data

assembled during a survey covering most of the Lower Peninsula of Michigan (Murchie, 1956) and from observations made on the E. S. George Reserve, Livingston County, Michigan. The University tract in Cheboygan County is located phytogeographically in the transition zone between the northeastern coniferous forest and the central or deciduous forest province to the south. The entire area has been glaciated several times. Characteristic of a glaciated region, the land is not deeply dissected but presents rolling contours with numerous lakes and bogs. Originally forests of pine and beech-maple dominated; removal of the pine in the decade following 1880, together with severe and recurrent fires, resulted in the establishment of an aspen association. Subsequently harvesting of hardwood and burning extended the aspen cover (Donahue, 1936).

Soils of the study area are sands (Roselawn, Rubicon, and Grayling) and sandy loams (Emmet); peats, mucks and clay loams occur as local deposits. In northern Michigan, soil formation through the

Fig. 1.—View in aspen forest, University of Michigan Biological Station, Cheboygan County, Michigan, showing characteristic forest floor conditions.

podzolation process is general. The humus layer is of the mor-type development with both A_{00} and A_0 strata present. By mid-summer, leaf-fall of the previous seasons forms a compact mat; below this, in the upper A_0, increasing fragmentation occurs, and some mineral soil, animal excreta, and roots mix with leaf fragments forming a dark brown to grey-black mineral soil in considerable amount mixed with consolidated organic substances. The zone of elluvial development (A_2) varies from a fibrous, gray, powdery layer with small amounts of mineral soil, to a whitish sand with little fiber. The former condition prevails in soil depressions and beneath heavier litter accumulations. The elluvial stratum rests on a yellowish to yellow-orange B-layer of sandy soil, and this, at varying depths, shades into the white, sandy, parent material. Major variation, aside from local drainage conditions and slope, relates to the amount of accumulated leaf material. The

Fig. 2.—View in upland forest of E. S. George Reserve, Livingston County, Michigan, showing type of forest floor condition which can sustain *Bimastos zeteki*.

forest floor has many pockets, from slight depressions to deep (60-70 cm) troughs.

No agricultural activity has been carried on within the study area, and it has not experienced significant fire damage for at least 30 years. Fallen trees, decaying limbs, and leaf deposits have been relatively undisturbed for long periods (Fig. 1). It is rather interesting to note that similar undisturbed soils on the E. S. George Reserve, with mull-type development, also support *Bimastos zeteki*. Here, as elsewhere, it is logs and litter with which the species is associated (Fig. 2).

Aspen predominates in the Cheboygan County area in which *zeteki* was studied. The trees are not large, but cover is frequently dense because of the number of trees present. Local variations in drainage, soil type, or age of stand finds the aspen replaced by pine or hardwood.

CLIMATE

The climate has been characterized (Foster *et al.*, 1939) as having:

> long cold winters, short cool summers, mild autumns, late cold springs, long days of sunshine during the summer, prevailing westerly winds, low evaporation, and an average of about 26 inches of rainfall. Hail storms, sleet storms, and destructive winds are very rare.

In general, the seasons during which this research was accomplished showed a progressive drying of the litter. Very heavy rainfall did not reverse this cycle once it had been established, but wet springtime conditions did delay the onset of the drought. The significance of this drying cycle in the life history of *zeteki* will be described later.

METHODS

Primary emphasis was placed on field observations of the worms, their oöthecae, and burrows. Virtual destruction, or at least serious derangement of the habitat was caused by the collecting process; this necessitated direct and immediate interpretation of worm activities from the instant of exposure. Many repetitions of the collecting act were required and actually undertaken to establish the constancy or uniqueness of a specific activity. In a few instances, potential or actual habitat sites were marked for study at a later time; otherwise, worms were collected for fixation or experimental work. Successful laboratory cultures of *Bimastos zeteki* were prepared by placing worms in wide-mouth jars filled with leaf mold and mineral soil, moistened, and maintained at 22°C. Oöthecae were isolated on wet filter paper in small stender dishes to permit continuous observation.

Earthworm excreta, referred to as castings, have been used in a number of important studies in order to measure earthworm activities or to trace their movements (Darwin, 1881; Evans and Guild, 1947; Grant, 1956). Of particular interest in this regard is the statement by Wilcke (1956):

> In diesen Tiefen werden die Gänge mit ihren Exkrementen tapeziert, deren ausgangsstoffe dem A-Horizont entstammen. Ja, man kann

vielfach au der Farbe frischer Losung erkennen; welchem Herizont das entnommene Material zuzuordness ist.

Because of the particularly sharp lines of division between strata in podzolic soils, I found these castings to be of great value in tracing the movements of *Bimastos zeteki.*

DISTRIBUTION AND ASSOCIATED EARTHWORM SPECIES

Bimastos zeteki is generally defined as a species of forest soils, the specific habitat being "in the wood and under the bark of decaying logs and sometimes under the logs" (Smith, 1917). In wet spring months, *zeteki* may be found not only beneath and in such logs and litter accumulations, but at considerable distances into the general forest floor litter. Moreover, burrows of this species were traced into the subsoil about 50 centimeters; deeper penetration is probable, but soil conditions prevented identification beyond this level.

The tunnels are distinct, well-formed, and, to judge from the castings, reasonably permanent.

By tracing these castings it was found that *Bimastos zeteki* passes back and forth from the inner parts of a moist log to the upper soil along fixed channels or burrows, the direction and amount of movement being no doubt related to moisture and food conditions. Similar migrations prevail in litter accumulations.

Drying of the leaf layers, humus, and upper soil during the summer months more and more restricts this earthworm to segments of the habitat retaining some moisture. Increasing use is made of the inner tissues of rotted logs, and only an occasional worm occurs in lenses of leaf litter which are damp. When desiccation of the latter becomes complete, no trace of *zeteki* can be found except for oöthecae from which young have not emerged.

No attempt was made to establish population density. Determinations made during routine work had to be circumscribed with qualifications to a degree which seriously reduced the usefulness of the data. As would perhaps be expected, *zeteki* is strikingly discontinuous in distribution; a day's field study might cover several acres with fewer than a dozen specimens to show for the work. On the other hand, 17 individuals were collected in one instance from a single log measuring approximately 75 cm long and 15 cm in diameter. More commonly, from one to four worms occupied a log or litter pile.

Dendrobaena rubida (Savigny) forma *tenuis* (Eisen) [= *Bimastos tenuis* (Eisen)] was the only oligochaete occurring consistently with *Bimastos zeteki* in the area considered here. *Allolobophora caliginosa* (Savigny), *Lumbricus rubellus* Hoffmeister, *Bimastos parvus* (Eisen) [= *B. beddardi* (Michaelson)], *Dendrobaena octaedra* (Savigny) and *Bimastos longicinctus* Smith and Gittens were found in the same woodlot as *zeteki* in various sections of the state of Michigan; rarely, however, were they taken from the same log or litter accumulation.

Activities and Movements

Crawling activity of *Bimastos zeteki* is of the typical lumbricid type but the movements are rather sluggish. Exposure of the animal seldom invokes rapid escape movements; immediate response is a shortening of the body followed by gradual withdrawal to cover. When some form of protection such as the burrow or surface debris is reached, the worm will usually slow or stop its movements, often for a considerable period. When *zeteki* is touched, vigorous escape reactions may occur. These are of three types: (1) rapid lashing of the body, (2) exudation of coelomic fluid, and (3) less commonly, posterior autotomy. If an individual is pricked sharply or handled roughly, it responds with a series of lashing movements reminiscent of certain species of *Pheretima* or *Eudrilus*. In this, the entire body is involved forming a U-shape first to one side, then the other, with a slight pause between twitches. From three to ten movements of this type will occur in succession.

With or without this lashing action, *zeteki* can eject a yellowish-white coelomic fluid from the dorsal pores. Anteriorly, intersegmental furrows 3/4, 4/5, and 5/6 are involved; posteriorly, the exudate issues from the subterminal three to five intersegmental furrows. To me, this fluid is odorless and tasteless. The salamander, *Plethodon cinereus,* upon which the substance was applied experimentally, evidenced no distress. After the initial response, a stronger stimulus, such as a needle prick, is necessary to cause *zeteki* to emit this fluid.

Stephenson (1930) has summarized the literature on autotomy among earthworms and suggests it is an indication of approaching death. Larger individuals of *Bimastos zeteki* possess a distinctively club-shaped terminal region of about 15 segments which the worm may cast, completely or in part, when subjected to some form of disturbance. Experimentation with specimens of *zeteki,* however, showed autotomy occurred in nearly all sizes and thus is apparently independent of age. Grasping the worm at the third subterminal segment caused the animal to cast from six to ten segments. If impaled anywhere between the fifth to the tenth subterminal segment, casting involved a total of thirteen segments. This casting power diminished anteriorly but was still evident at subterminal segment 32, in which case the worm broke at segment 33. The anterior region did not respond in this fashion.

Lashing, exudation, and autotomy may serve *Bimastos zeteki* as survival mechanisms in the face of predation. Burrows of small mammals abound in the areas inhabited by this oligochaete; likewise, *Plethodon cinereus* is abundant. Attempts to feed *zeteki* to the latter were inconclusive. At present, the geographic origins of *zeteki* are unknown; thus, the possibility exists that the protective devices may have arisen in connection with a different faunal complex.

Somite Numbers and Regeneration

A summary of somite counts on 161 field collected specimens and 41 individuals killed and fixed immediately after their emergence from oöthecae is presented in Figure 3. Specimens showing autotomy due to collecting were not considered. Smith (1917) gave the range of somite numbers for *zeteki* as 100 to 142 and stated that "in complete specimens the number usually exceeds 130." Gates (1956) established limits of 126-154 but presented additional tabular data on 26 specimens indicating a range from 94 to 154. Of these, a goodly number were designated as "amputee."

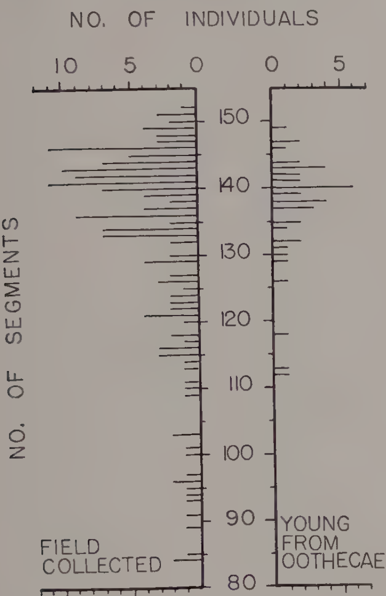

Fig. 3.—Comparison of segment numbers in field collected specimens with those reared from oöthecae in the laboratory.

With regard to regeneration in *Bimastos zeteki,* Gates (1956) has written:

> "An anal segment had been reconstituted in each of the posterior amputees. No other regeneration had taken place though amputation in some of the cases certainly had not been recent."

He further indicates that posterior regeneration may not be possible for *zeketi* under normal conditions. Similarly, I observed no posterior regeneration in Michigan material collected in the field, nor was I able to induce such regeneration in laboratory cultures.

On the basis of information now available, Gates' inferences on segmental numbers of 126-154 and the probable lack of capacity for posterior regeneration by *Bimastos zeteki* do apply to Michigan representatives of the species. It appears likely that post-emergent growth does not occur, and thus, the definitive number of segments

is present at the time *zeteki* leaves the oötheca; subsequent growth is simply by enlargement of existing segments. It is to be expected that a population composed of larger numbers of older worms would have a larger proportion of amputees; from this it follows that segment-number counts may afford a generalized measure of the age of a population.

Periodicity

Field evidence obtained in the course of this investigation underscores the strong influence of environmental factors on oligochaete periodicity. Of these, moisture is the most significant. The litter of upland forest areas in Cheboygan County dries out thoroughly by mid-summer. This includes thick accumulations as well as the general forest floor, although lenses of dampness may persist in the compressed leaf zone for some weeks. The under surfaces of logs dry out in similar fashion, approximating conditions in litter piles. Pulpy inner layers of such logs, especially *Betula* and *Populus,* do remain saturated with moisture for long periods, and a substantial number are quite wet through late summer and fall months. Insufficient evidence is available on winter conditions to permit description of the hibernal aspects of the *zeteki* activity cycle.

Table I summarizes the Cheboygan County records of *Bimastos zeteki* for 1957. Immediately following the snow-melt in April, worms were quite scarce. The only clitellate specimen was found beneath a small aspen log on an open slope with southern exposure. From the

TABLE I.—Field collections of *Bimastos zeteki* for 1957, listed by number of individuals in each weight class.

Weight in grams	April 27	May 10	May 25	June 11	June 24	June 27	June 28	July 4	July 5	July 10	July 18	July 24	July 25	Aug. 1	Aug. 9	Aug. 14
1.51-1.60				1*	1	1										
1.41-1.50		1*														
1.31-1.40																
1.21-1.30			1*			1										
1.11-1.20	1*					1										
1.01-1.10		1		1*			1					1		1		
0.91-1.00		1*				1	1									
0.81-0.90			1*	1					2*			1				
0.71-0.80		1*					1		1*	1*	2			1	2	1
0.61-0.70			1*			1	1			3	3	1	4	2	1	1
0.51-0.60			1		1	1			1	2	6			2		7
0.41-0.50			1	2		3		1	1	2	1	1	5		1	5
0.31-0.40			1			7		2		1	2		2		2	3
0.21-0.30	1	2	4	1	1	5		3		2	1		1	1	1	1
0.11-0.20	3	2	2	1	2	1	1		1			1	1		1	1
1.01-1.10												3	1			

* Clitellate individuals.

second week of May, through mid-June, 1957, larger clitellate individuals were reasonably common in the study area. During this period, *zeteki* was to be found in the widest variety of habitats; small branches, logs, or bark fragments scarcely five centimeters in diameter provided suitable cover. Moreover, worms ranged out from litter accumulations or logs into the thinner humus layer of the forest floor. Oöthecae were abundant by late May, and in abundance through June. Disposition of these structures will be considered in a later section of this paper.

Size of the clitellum was used to describe the degree of sexual development, inasmuch as internal structures (seminal vesicles, male funnels, etc.) provide no clear evidence in this regard. Gates (1956) concluded that *zeteki* is probably male sterile and thus parthenogenetic. After mid-July, I could not find any *Bimastos zeteki* in the clitellate (presumed reproductive) state. Individuals which did show some degree of clitellar development were either quite obviously immature or regressive. The latter is signaled by the appearance in the swollen clitellum of whitish pustules which subsequently spread to other parts of the worm's body. There is no pattern to this invasion, nor is the density uniform among several worms. Excepting these reproductive individuals and the very largest worms, the data assembled in Table I do not show an over-all reduction in population numbers through the season. Larger individuals of this surviving population did show traces of pigmentation in the clitellar zone, but no glandular development was evident.

It may be noted (Table I) that small worms comprised a substantial part of the total population in April and May, 1957. This group unquestionably over-wintered, having emerged from oöthecae in late summer months of 1956. These emergees, plus those emerging in spring and early summer months of 1957, would, I believe, form the potential reproductives of the next season.

Climatic influences may displace cyclic tendencies which might otherwise be expressed by *Bimastos zeteki*. A late cold spring would thus delay deposition of the oöthecae, while severe drought at any time during the warmer months will reduce the space available for *zeteki* and cause it to migrate into the sub-soil or sections of the habitat with high water-retaining capacity. I have never observed this species in an inactive, quiescent state (= diapause of some authors) in the field, nor could the condition be induced in laboratory cultures. Migration is thus the only apparent survival mechanism utilized by *zeteki* during periods of environmental stress and, in this, there appears to be no inherent rhythm.

OÖTHECAE

The oöthecae of *Bimastos zeteki* are distinctive and unlikely to be confused with those of any other Michigan earthworm species (Fig. 4B). When new, they are greenish yellow, becoming yellowish with development; empty structures are amber. Weights of 22 oöthecae ranged from 0.04 to 0.14 grams with an average of 0.079 grams;

lengths varied from 5.0 to 8.5 mm and widths from 4.5 to 7.0 mm, with averages of 6.7 mm and 5.6 mm for length and width, respectively.

Commonly *zeteki* encapsulates the oötheca in a solid covering of soil (Fig. 4A). In the field condition, this soil capsule with its contained oötheca may weigh from 0.5 to 1.5 grams and measure approximately 15 centimeters in diameter. Murchie (1955) has reported a similar behavior of *Allolobophora muldali* (Omodeo). More recently, Christensen (1956) described encapsulation of oöthecae in *Enchytraeus albidus* Henle (Enchytraeidae) in which deposition of the soil is oral. No conclusions can be drawn as to the method by which *zeteki* applies soil to the capsule. Moreover, this species does not always cover the oötheca completely; the latter may be pressed to the substrate with a soil coat over the upper or free surface only. Sometimes, no soil capsule is present.

Whether covered or free, oöthecae are usually placed along the sides of formed burrows, between leaves, under logs, or within the tissues of decaying logs. One capsule was found beneath the moss cover on a tree trunk about 15 cm above the soil surface. Selection of the site for oöthecal deposition is seemingly dependent upon random movement of the worm in response to favorable conditions in the habitat, especially moisture, perhaps reinforced by stimuli of which we as yet know little. This hypothesis is strengthened by the observation that oöthecae are less frequently found alone than in "nests" of from two to five individual capsules. All of these may lie within an area no more than 75 cm² in extent. With rare exception, only one fully clitellate worm is to be found near such a "nest."

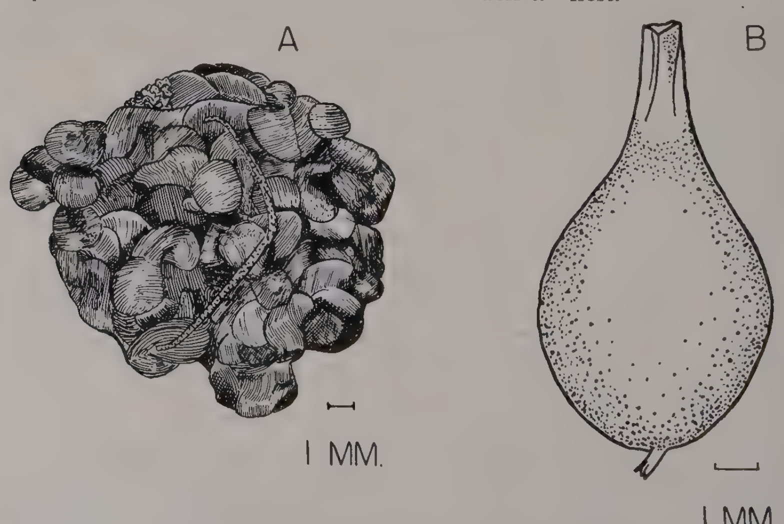

Fig. 4.—Oöthecae of *Bimastos zeteki*. A. External view with capsule of soil. B. External view without soil capsule.

Stages of development among the capsules of a clutch or nest invariably show some variation as evidenced by size of the contained young. This indicates an extended reproductive period for *zeteki* as well as the probability of semi-permanent occupancy of certain sections of the tunnel system.

Accumulated laboratory evidence shows that *zeteki* has an intra-oöthecal period of about three weeks. To determine the effects of soil climate on oöthecal life, ten field-collected capsules, all containing well-developed, living young, were placed in moist containers and maintained at 6° C for five weeks. Worms emerged from one capsule at the end of the first week and from a second on the day before the refrigerated period was terminated. Of the oöthecae brought to room temperature, three were destroyed because of excessive dryness; worms emerged from the remaining five within four days.

Field collected oöthecae showed a remarkable tolerance to desiccation; in many instances, shrunken and folded capsules were found to continue development when water was added to their environment. In the laboratory, capsules were dried and re-wet to determine their ability to survive. Normal development was possible after a weight loss of 54 percent.

No precise data are available concerning the time of year oöthecal deposition begins. Capsules could not be found in the Cheboygan County area on April 27, nor May 10, 1957. However, one individual in the May 10 collection did produce an oötheca; this occurred while the animal was still in the collecting bottle.

In northern Michigan, temporary inhibition of oöthecal development is likely to occur in early spring months due to lowered soil temperatures. Extension of intra-oöthecal life is probably of no great consequence except under severe drought conditions. Moisture deficiency should be considered a mortality factor for the oöthecae of *zeteki*, but variations are so great, both in conditions and effects, that generalizations are not possible.

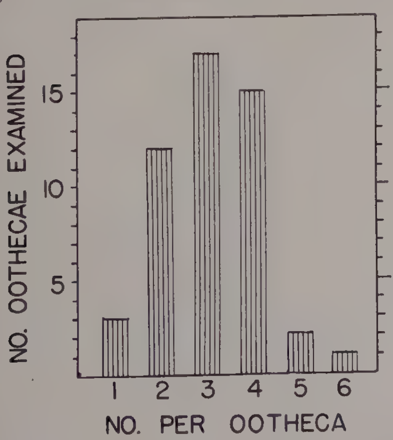

Fig. 5.—Graphical representation of data on counts of young emerging from oöthecae of *Bimastos zeteki*.

The number of young *Bimastos zeteki* per oötheca is variable (Fig. 5), two, three, or four being the most common number. Single emergees were nearly twice the size of "normal" individuals (60 mm versus 35 mm average). Moreover, in laboratory cultures, as much as four days separated the emergence of first and last worms from one capsule.

GROWTH RATE

Measurements of individuals from field populations afford few criteria for appraising growth rate in *Bimastos zeteki.* Despite the risk involved in extrapolation from laboratory results to explain conditions in nature, it was considered essential to obtain some approxi-

TABLE II.—Growth of *Bimastos zeteki* from 7 oötheca (A-G) in laboratory cultures of mixed soil and litter

Culture	Initial wgt. (gms.)	Aug. 10	Sept. 15	Nov. 27
	July 14, 1956			
A-1	0.053	0.284	0.64	0.95
A-2	0.039	0.233	0.51	0.84
A-3	0.048	0.259	0.69	1.10
	July 15			
B-1	0.036	0.224	0.40	0.72
B-2	0.035	0.229	0.59	0.67
B.3	0.039	0.194	0.54	0.77
B-4	0.040	0.213	0.60	0.92
C-1	0.024	0.137	0.29	0.44
C-2	0.028	0.096	0.25	0.72
	July 16			
D-1	0.038	0.248	0.62	0.92
D-2	0.032	0.266	0.75	1.00
D-3	0.030	0.186	0.69	0.98
D-4	0.028	0.230	0.65	1.01
	July 20			
E-1	0.029	0.145	0.50	0.90
E-2	0.028	0.198	0.60	0.97
E-3	0.025	0.095	0.31	0.66
E-4	0.036	0.121	0.47	0.86
	July 22			
F-1	0.027	0.126	0.59	1.35
F-2	0.048	0.168	0.70	1.37
G-1	0.031	0.105	0.57	1.42
G-2	0.030	0.125	0.42	0.74
G-3	0.022	0.110	0.64	1.88
G-4	0.022	0.134	0.64	1.24
G-5	0.022	0.166	*	*
G-6	0.010	*	*	*
Mean	0.032	0.178	0.55	0.97

* Worm not recovered.

mation of growth rate which *zeteki* might show during the three or four month post-emergent period.

Accordingly, in 1956, individual worms were isolated in two major culture series. In the first, 25 young from seven oöthecae were each isolated in an organic, soil-litter mixture. This mixture, it was hoped, would provide the major nutritional components required by the species and utilized by it in nature. The second series involved 30 worms placed on six selected substrates: (1) wet aspen leaves from the compressed leaf zone, (2) organic, loamy-sand soil with some leaf mold, (3) silt loam, (4) soil from matted zone, (5) sandy soil from "B" horizon, and (6) wood and bark of a *Betula* log. Five replications were made of each substrate type.

All cultures were kept moist and maintained at a temperature of 22-26° C. Worms reared on the mixture of soil and litter show (Table II) an average thirty-fold weight increase during a period of from 97 to 105 days. The increase in mean weights, 0.032 to 0.97 gms, indicates clearly that *Bimastos zeteki* could reach reproductive size during a three or four month period.

Among the cultures of the selected substrate series (Table III), only two, the organic, loamy sand and the soil from the matted root zone, gave growth results for *zeteki* which approximated conditions in the soil-litter mixture. As a matter of fact, the apparent intercultural growth differentials exhibited by this series were most interesting. For example, the two worms which survived in the culture of sand from the "B" horizon did not quite double their weight whereas individuals in an organic, loamy sand soil increased, on the average, nearly 40 times their original weight. Statistical analysis (Table VI) of the estimate of variance between the results from the soil-litter mixture and the complete series of selected substrate types gave a variance ratio which was significant at the 4 percent level ($F = 2.26$).

In repeating this laboratory experimentation in 1957, special attention was given to the effects of substrate type on earthworm growth. As in 1956, two culture series were established. For one of these, I used a screened, loamy-sand soil from which very uniform replications could be made. Ten emergees from three oöthecae were each isolated in 50 grams of this soil type.

Materials for the varied culture types (leaves, wood pulp, etc.) were also selected with greater care to avoid contaminants and five replications of each type established as follows: (1) an organic, loamy-sand soil, (2) pulpy wood from the interior of a *Betula* log, (3) soil from matted root zone, (4) leaf mold, (5) leaves from compressed leaf zone, (6) surface leaves of previous year's fall, and (7) sand from "B" horizon. A single, newly emerged worm was isolated in each of these. Because of the number of young involved and the high temperatures prevailing in the laboratory, no individual initial weights could be taken, however, an average initial weight of approximately 0.03 grams may be assumed.

TABLE III.—Growth of *Bimastos zeteki* in laboratory cultures of different substrate types. Five replications (a-e) of each culture type

Culture	Initial Wgt. (gms.) July 24, 1956	December 12	Substrate type
a	0.024	0.48	
2	0.019	0.48	
c	0.039	0.50	Leaf litter
d	0.023	0.37	from compressed leaf zone
e	0.030	0.53	
Mean	0.027	0.47	
a	0.087	0.32	
b	0.030	*	
c	0.030	*	Silt loam soil
d	0.052	0.14	
e	0.036	*	
Mean	0.047	0.23	
a	0.083	*	
b	0.042	0.09	
c	0.032	*	Sand from "B" horizon
d	0.025	0.06	
e	0.035	*	
Mean	0.0434	0.075	
a	0.090	1.64	
b	0.025	1.37	
c	0.044	1.52	Organic, loamy sand
d	0.014	1.62	
e	0.042	1.38	
Mean	0.043	1.50	
a	0.091	0.85	
b	0.043	0.75	
c	0.033	0.82	Soil from matted root zone
d	0.035	0.63	
e	0.044	0.63	
Mean	0.049	0.73	
a	0.026	0.40	
b	0.039	0.41	
c	0.027	0.48	Wood and bark, *Betula* log
d	0.032	0.63	
e	0.034	0.68	
Mean	0.031	0.52	

* Worm not recovered.

All cultures were uniformly moistened and maintained at 22-26° C. for the duration of the experiment. The results are included in Tables IV and V. Even cursory examination of these data reveals a high correlation between substrate type and the growth rate of *Bimastos zeteki.* Analysis of the estimate of variance (Table VI), based upon the uniform soil type (Table IV) and the selected culture types (Table V), shows a highly significant ratio at the 1 percent level ($F = 136.32$). It may be concluded that growth of *zeteki* is substrate dependent. These results corroborate the findings of Moszynski (1934) who pointed out that soil exerts its influence not only in determining the number of earthworms living there but also their size. He further stated that under favorable ecological conditions the worms are much larger than when unfavorable conditions prevail.

The 1957 cultures were concerned less with growth rate *per se* than with growth differentials which might be attributed to the substrate. It may be noted, however, that the worms reared in the organic, loamy-sand soil (Table V) did show an average weight increase of more than seventy-fold. Again, the fact is underscored that *zeteki* can attain full size within four months if suitable conditions obtain in the environment.

Inasmuch as the aims and procedures used in the two seasons (1956, 1957) of laboratory work were somewhat different, no direct comparison between them will be made here. Moreover, I believe it would be unwise to generalize from these laboratory findings to define a "best" substrate for *Bimastos zeteki.* The worms placed in nearly pure sand did indeed show little or no growth and it could reasonably be concluded that too little organic material was available to serve as food for the worms. In cultures of unconsolidated leaf litter from both the compressed leaf zone and the surface leaf fall, cultures high in organic matter, the average weight increases for *zeteki* were twenty-six and thirteen fold respectively. Moreover, worms in organic, loamy sand increased their weight, on the average, 77 times.

TABLE IV.—Growth of *Bimastos zeteki* from 3 oöthecae (A-C) in laboratory culture on uniform substrate

Culture	Initial wgt. (gms.) July 9, 1957	July 22	Aug. 12	Oct. 15
A-1	0.019	0.064	0.294	0.47
A-2	0.018	0.056	0.195	0.47
A-3	0.022	0.059	0.263	0.59
A-4	0.024	0.052	0.254	0.61
B-1	0.032	0.070	0.251	0.56
B-2	0.026	0.047	0.260	0.56
B-3	0.033	0.070	0.224	0.56
B-4	0.029	0.084	0.239	0.55
B-5	0.030	0.069	0.237	0.57
C-1	0.041	0.057	0.211	0.48
Mean	0.027	0.062	0.24	0.54

TABLE V.—Growth of *Bimastos zeteki* in laboratory cultures on different substrate types; five replication (a-e) of each culture type

Culture§	Aug. 13	Oct. 15	Substrate type
a	*	*	
b	0.81	*	
c	1.24	2.46	Organic soil, loamy sand
d	0.94	2.08	
e	1.61	2.41	
Mean	1.83	2.31	
a	*	*	
b	*	*	
c	*	*	Pulpy wood *Betula* log
d	0.03	*	
e	*	*	
Mean	0.03		
a	0.43	0.91	
b	0.42	0.74	
c	0.74	1.17	Soil from matted root layer
d	0.60	0.95	
e	0.60	1.01	
Mean	0.58	0.95	
a	0.55	1.03	
b.	0.58	0.84	
c	*	*	Leaf Mold
d	0.41	*	
e	*	*	
Mean	0.51	0.93	
a	0.28	0.70	
b	0.36	0.74	
c	0.46	0.77	Leaves from compressed-leaf zone
d	0.47	0.98	
e	*	*	
Mean	0.39	0.79	
a	0.10	0.49	
b	0.09	0.32	
c	0.11	0.37	Surface leaves, previous year's fall
d	0.10	0.41	
e	0.12	0.49	
Mean	0.10	0.41	
a	*	*	
b	0.02	*	Sand from "B" horizon; 10″ depth
c	0.04	*	
d	*	*	
e	0.05	*	
Mean	0.036	*	

§ Experiment started June 28, 1957; avg. initial wgt. assumed at 0.03 gm. per worm.

* Worm not recovered.

Apparently it is not the absolute amount of organic material present per unit volume of soil that is critical. Rather, the essential ingredients for growth must be available to the worm and these food elements have to be in some form which the animal can use. Pure wood pulp, freshly fallen leaves, and similar substances, although very high in the organic fraction, may require substantial modification by other biotic elements before *zeteki* can utilize them for food. Nutritional aspects of earthworm biology have not been worked out in any detail insofar as I am aware. Many problems relating to habitat occupancy by earthworms, as well as their regional distribution, may be solved when more information is available on the precise trophic levels occupied by earthworms.

The laboratory results do enable us to make more adequate interpretations of field data. Forest areas in northern Michigan provide a variety of substrate types in many combinations. *Bimastos zeteki* will move through these potential habitats, selecting, I believe, those which it can utilize with the greatest efficiency. As stated previously, habitat availability for *zeteki* varies with moisture content of soil and litter. In the drying cycle, this worm will, perforce, move into a niche providing the most stable moisture regime. Under such circumstances, something less than satisfactory nutritional levels may obtain but survival is possible even though growth will be reduced for an extended period.

A drought enforced migration sends the worms either downward

TABLE VI.—Analysis of estimate of variance of growth rate of *Bimastos zeteki* as related to substrate type

Source of variation	Degrees of freedom	(S^2) Estimated variance	F ratio	P – value
1956 Mixed soil (Table II)	22	0.098		
1956 Selected substrates (Table III)	23	0.222	2.26*	P= .04
1957 Uniform soil (Table IV)	9	0.003		
1957 Selected substrate (Table V)	18	0.409	136.33**	P< .01

* When $N_1 = 23$ and $N_2 = 22$; for $P = 0.05$, $F = 2.04$; for $P = 0.01$, $F = 2.79$.

** When $N_1 = 18$ and $N_2 = 9$; for $P = 0.05$, $F = 2.95$; for $P = 0.01$, $F = 4.86$.

into the subsoil (B-horizon) or into wet inner tissues of logs. The period of soil moisture stress, insofar as *zeteki* is concerned, may include middle to late summer and fall months. I have not been able to collect the species during the winter months and it is probable that *zeteki* is not able to occupy the upper organic soil layer during the cold period.

Thus, the 1957 collection records for *Bimastos zeteki* can be described in terms of three major elements: (1) large, over-wintering, clitellate worms; (2) over-wintering, aclitellate worms (1956 emergees); and (3) aclitellate worms which began their emergence from oöthecae during May of 1957. By late July or early August, many of the early 1957 emergees are indistinguishable from the over-wintering 1956 emergees, at least from the standpoint of size. Small worms which winter over and those which emerge from oöthecae early in the spring, may grow rapidly enough during the summer to attain full size and these worms, I believe, comprise the reproductives of the ensuing spring. Therefore, an individual worm may become reproductive at approximately 12-14 months of age, or, if it emerge from its oötheca at the beginning of a dry period, the reproductive state may not be reached until a lapse of 22-26 months.

Summary of Life Cycle

On the basis of existing information, a number of generalizations about the life history of *Bimastos zeteki* may be made. Obligatory parthenogenicity is probable, with oöthecal deposition occurring through late spring and early summer. Lowered soil temperature and drought may inhibit intra-oöthecal life or delay the time of emergence. Assuming four viable oöthecae per adult, and three young in each capsule, approximately twelve offspring per reproductive worm are produced. It is not known whether or not *zeteki* can live and produce oöthecae more than once.

Worms emerging from oöthecae in early summer could, I believe, become reproductive during the spring of the ensuing year, whereas emergees of the mid-summer period very likely do not attain full growth until the end of the following summer and thus are clitellate in their second spring.

The basic two-season life cycle outlined here may vary significantly due to extrinsic factors of the soil climate. This is true moreover within a single region or population; departure from the patterns described for northern Michigan, is quite possible in populations of other areas.

Conclusions

As mentioned earlier in this paper, characterization of the biology of an oligochaete is hazardous if strictly regional studies are applied to the species in general, regardless of habitat occupancy. As a matter of fact, some Lumbricidae show an amazing degree of tolerance in their use of different segments of the soil environment. Part of this may be explained as the principle of ecological equivalence and to the

physiological adaptability of earthworms. Further, both field and laboratory observations are somewhat subjective inasmuch as the investigator must make interpretations within the range of his experiences. *Lumbricus terrestris*, for example, so often identified as an inhabitant of field and pasture soils, thrives in moist ravines, woodlands, or in river forests of Michigan. Here, like *Bimastos zeteki* it moves freely through leafy accumulations, beneath logs, or similar debris. If we view *terrestris* as a forest species, if indeed not as a litter inhabitant, many behavioral patterns it exhibits in field or pasture may be seen as accommodations to the leafless environment.

Precise trophic levels are largely unknown for earthworm species. Here again, presumed competition between species has been related to population density or habitat occupancy *per se* but not, insofar as I am aware, on the basis of their exact nutritional requirements. Unknown also are the effects of inhibitory or repellent substances produced by worms, which might cause intraspecific responses such as dispersion. Observed variations in size of young *zeteki* in a series of oöthecae are obviously due to polyembryony but whether based upon nutrition or inhibitory mechanisms such as those described by Rose (1959) for tadpoles, has not been established.

Within the family Lumbricidae, considerable uncertainty prevails concerning geographic and environmental origins of species. Thus, although many activities of *Bimastos zeteki* are common to nearly all earthworms, it is possible that some of its rather specialized reactions have their source far removed from existing conditions.

On the basis of information now available to us concerning the biology of *Bimastos zeteki* in Michigan forest soils, the species may be considered clearly adapted to the soil-litter zone. Its presence there is independent of interspecific competition but is related to physical constancy of the habitat. Thus, the environmental stability afforded by accumulated leaf layers or a log is itself of greater consequence to the worm than the nature of the super-imposed material. The data presented further substantiate the very strong control that soil climate imposes upon earthworm biology. The strength of such influence, insofar as *zeteki* is concerned, raises doubts as to the efficiency if not the very existence of cyclic phenomena regulated by internal rhythms of earthworms.

SUMMARY

Salient features are presented on the life history of *Bimastos zeteki* Smith and Gittins (Lumbricidae) based upon field and laboratory study over a period of three summers. This species is an inhabitant of the soil-litter zone; it has an apparent two season life cycle which is strongly influenced by vicissitudes of soil climate. In late spring and early summer, each mature individual of *zeteki* may produce from two to five oöthecae; these are polyembryonic, with generally two, three, or four young surviving to emerge. Normally, oöthecae are encapsulated with soil and placed in burrows immediately beneath leaves or a log. Reproductive worms are common in spring and early

summer; no fully clitellate individuals were encountered in Michigan collections after the end of July. Growth is rapid; worms may achieve virtually full size within four months from the time of emergence. Growth rate is seemingly substrate-related and, insofar as Michigan forests are concerned, substrate availability depends upon soil moisture. Migration is the only known response of *Bimastos zeteki* to water loss. Young emerge from oöthecae with the full complement of segments; autotomy of terminal segments is readily induced but posterior regeneration has not been observed. On the basis of available information, *zeteki* may be considered an indigenous element of the forest soil-litter complex of Michigan.

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Artificial Hybridization of the Gray Treefrog, Hyla versicolor (Hylidae)[1]

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This is a communication of results obtained from artificial hybridizations between the gray treefrog (*Hyla versicolor*) and certain other anuran species. All of the eggs used in these crosses were obtained from a single female *H. versicolor*. Fertilization was attempted with sperm from males of the following species: *H. baudini, H. versicolor, H. squirella, H. cinerea, Pseudacris clarki, Acris crepitans, Bufo compactilis* and *Gastrophryne olivacea*. Our objectives were to find out if reproductive isolation is a factor in preventing gene exchange between *H. versicolor* and some of the related species with which it is sympatric and to determine the extent to which hybridization is possible between certain species of varying degrees of relationship.

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Methods

Ovulation was induced by introduction of two anterior pituitary glands (from adult male *Bufo valliceps*) into the peritoneal cavity. Laying began approximately seven hours later. Sperm suspensions were prepared from testes of the various males in the manner described by Rugh (1948) using about 10 cc of aged tap water for each suspension. Eggs were passed from the female, held in vertical position, directly into each sperm preparation. The female was thoroughly washed with tap water after each "laying" in order to eliminate the possibility of introducing alien sperm into succeeding preparations.

Developing embryos were placed in enamel pans (16 x 10 x 2.5 inches) containing aged, aerated tap water. After hatching, the tadpoles were transferred to 10- and 15-gallon aquaria and were fed boiled lettuce and, occasionally, strained spinach. Shortly before metamorphosis began, wooden chips were placed in the tanks for emergence of the young frogs and the tanks were covered with cheesecloth to prevent their escape. Young frogs were maintained on damp soil, two to four inches deep, in standard aquaria of the sizes given above. They were fed small insects (*Drosophila*, homopterans and hemipterans) and mealworms (*Tenebrio*).

Results of the crosses are summarized in Table I.

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INTRAFAMILIAL CROSSES

♀ *Hyla versicolor* x ♂ *H. baudini*.—A few abnormal cleavages were noted in stages preceding blastulation, but most of the early embryos appeared normal. One hundred and sixty-four tadpoles hatched beginning on the third day after fertilization, but most of these died within one week after hatching. The surviving tadpoles grew to approximately twice the maximum size of controls, possibly due to less crowded conditions. Metamorphosis of 10 individuals occurred from 30 to 50 days after fertilization. Except for their large size, the young hybrids were very similar to the control animals (Fig. 1A, B and C). One hybrid lacked an eye and another had an elongated lower jaw which protruded beyond the rostrum. The head of the latter appeared slightly asymmetrical when viewed from above and one of the eyes was situated a little farther posterior than the other.

The young hybrids were bright green at metamorphosis and were either green or gray later on. They did not assume the brown or yellow-brown commonly seen in *H. baudini*.

One and probably both of the males that survived to sexual maturity began calling less than four months after fertilization. The throats were moderately pigmented and microscopic examination of thin sections of the testes revealed apparently normal spermatogenesis, as in the controls. These frogs survived a little over 10 months but both died before back-crosses could be attempted. Snout-vent lengths after preservation were 36.5 mm and 38.7 mm. Both specimens had large fat bodies.

A third surviving individual had a lightly pigmented throat and before death was assumed to be a female. After it died, examination of the viscera revealed the enlarged gonads to be irregularly oval, translucent, fluid-filled sacs. Rupture of the tough surrounding membrane liberated a straw-colored fluid. Oviducts were not present. Microscopic examination of thin sections of the left gonad showed that gametogenesis was not occurring. This individual lived 9 months and 27 days from the time of fertilization and attained a snout-vent length of 41.5 mm (measured after preservation). The fat bodies were well developed.

♀ *Hyla versicolor* x ♂ *H. versicolor* (control).—No abnormalities were observed in early developmental stages. Hatching began on the third day after fertilization. Of 237 young tadpoles, only 74 transformed. Under crowded conditions, rapid accumulation of wastes in the latter part of the tadpole stage probably accounts for the high mortality. Two of the newly metamorphosed frogs were one-eyed, but all of the others appeared normal. Twenty-five young frogs died soon after metamorphosis and were not preserved and 34 others were released because of limitations on space and food supply. Of 15 frogs kept in the laboratory, five males reached sexual maturity and began calling about four months after fertilization. Microscopic examination of sections of the testis of an adult male revealed normal spermatogenesis. One female was evidently approaching sexual maturity at the

time of death. The ovaries of this frog were lobed, roughly oval in shape, granular and otherwise similar to those of wild-caught *H. versicolor* females, but they did not contain mature ova. All five females possessed oviducts.

The mean snout-vent length of the five males that reached sexual maturity was 31.2 mm (range, 30.1 - 31.9). The mean length of the

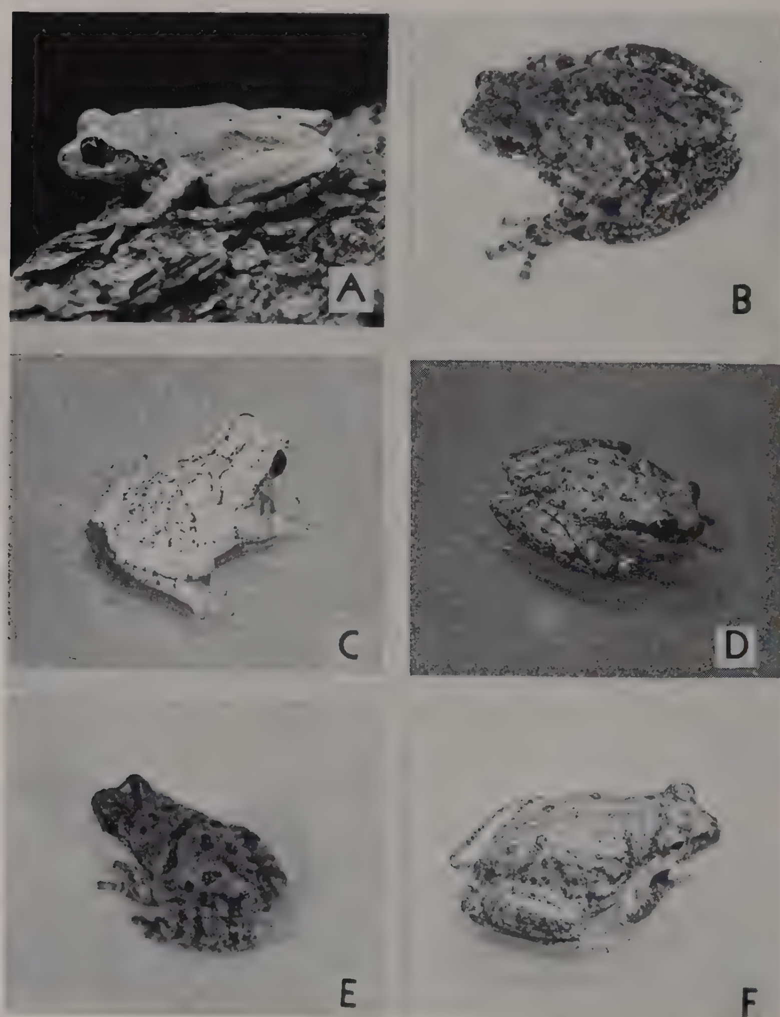

Fig. 1.—Photographs of hybrids and control. Not to same scale. A. ♀ *Hyla versicolor* x ♂ *H. baudini* hybrid. B. Same cross, different individual. C. *Hyla versicolor* control. D. ♀ *H. versicolor* x ♂ *Pseudacris clarki* hybrid. E. ♀ *H. versicolor* x ♂ *H. squirella* hybrid. F. Same cross, different individual.

left testis of the same five males was 3.6 mm (range, 3.2 - 3.8). The mean snout-vent length of all 10 males, after preservation, was 27.9 mm (range, 23.4 - 31.9); for the five females the mean snout-vent length was 25.0 mm (range, 23.0 - 28.2). Fat bodies were present in all 15 frogs.

♀ *Hyla versicolor* x ♂ *H. squirella*.—A small number of abnormal cleavages occurred in preblastula stages and a few post-gastrula embryos had distended bellies, but most developed normally. Three hundred and thirty-five tadpoles hatched on or before the fifth day after fertilization, while 16 others were still in tail bud stages on the fifth day. One hundred and sixteen frogs metamorphosed between 29 and 68 days after fertilization. Many of these young frogs died within a few days after transformation and were not preserved. Fifty-three frogs (preserved after death) survived from two to 24 months after fertilization. As in the controls, much of the tadpole and young frog mortality probably resulted from over-crowding.

One of the young frogs was without an eye, another had abnormally short femora which considerably reduced the distance it could jump, and a third had one of its eyes situated slightly more posterior than the other. All of the others were of normal appearance at metamorphosis.

The young hybrids were bright green immediately after metamorphosis but later their colors ranged through various shades of gray, green and dull brown. In size and body form, the adult hybrids were more similar to the male than to the female parental species, but they resembled *H. versicolor* in possessing a light subocular spot (Fig. 1E). Dark markings of the dorsum were variable but mostly intermediate between the extensive irregular blotches common in *H. versicolor* and the smaller spots at times seen in *H. squirella*.

Several male hybrids began calling less than four months after fertilization. These frogs had light to moderately pigmented throats. When an attempt was made to use one of them in a cross, the testes could not be located. Later it was discovered that the testes of this and several other individuals were imbedded in the fat bodies. In others, the testes were partially to completely free of the fat bodies. The testes of the adult hybrids were much smaller than those of controls of comparable size. The mean snout-vent length of five of the largest hybrid males was 30.3 mm (range, 30.0 - 30.9) and the mean length of the left testis of these five hybrids was 1.6 mm (range, 1.4 - 1.9). One male hybrid had only one testis. Microscopic examination of thin sections of the testes of two mature males with well developed fat bodies revealed that spermatogenesis was not occurring in either. The mean snout-vent length of 34 preserved males was 27.4 mm (range, 21.1 - 30.9).

Eight hybrid females possessed ovaries, oviducts and fat bodies, but all were immature at death. The ovaries did not contain mature eggs and the oviducts were small and relatively straight. The mean snout-vent length after preservation was 24.1 mm (range, 20.7 - 26.3).

The sex of the remaining 11 individuals was uncertain. Three of

these (snout-vent lengths 27.9, 27.5 and 27.4 mm) had well-developed fat bodies but had neither gonads nor oviducts; one (snout-vent length 25.0 mm) had only one gonad (structurally similar to the ovaries of controls), no oviducts and no fat bodies; two (snout-vent lengths of 25.5 and 22.8 mm) had such rudimentary reproductive structures that the sex could not be ascertained; and the sex of five specimens was unknown because of the poor state of preservation.

♀ *Hyla versicolor* x ♂ *H. cinerea.*—Some of the very early cleavages were abnormal. None of the tadpoles survived more than a few days after hatching, which occurred about the fifth day after fertilization.

♀ *Hyla versicolor* x ♂ *Pseudacris clarki.*—Difficulties during gastrulation resulted in most of the embryos having distended bellies. Hatching occurred about the fifth day after fertilization and six tadpoles transformed between 39 and 49 days after fertilization. Two of the young frogs failed to climb out of the water and were drowned shortly after metamorphosis. Two survived three and one-half months after fertilization but both were immature at the time of death. Their snout-vent lengths after preservation were 17.8 mm and 22.9 mm. They possessed neither gonads, oviducts nor fat bodies. The remaining two individuals survived longer and attained a larger size, but they were not discovered soon enough after death to be preserved. They were both believed to be mature at the time of death. A. P. Blair (Moore, 1955) also obtained adults from this cross.

In general appearance (Fig. 1D) and habit, the hybrids resembled *Pseudacris clarki* more so than *Hyla versicolor.* Unlike the controls,

TABLE I.—Results of laboratory crosses between a female *Hyla versicolor* from Bastrop County, Texas, and males of the species shown in the left hand column (counties in which the males were collected are given where these are known; all were collected in Texas).

Male	No. of eggs	Cleavage (%)	Hatched (%)	Metamorphosis (%)	Stage reached
Hyla baudini Cameron County	322	72.4	50.9	3.1	Adult
H. versicolor (control) Bastrop County	301	100.0	78.7	24.6	Adult
H. squirella	377	98.9	88.9[1,2]	30.8	Adult
H. cinerea	141	85.1	31.2[1]	—	Young tadpole
Pseudacris clarki Travis County	426	99.8	43.0	1.4	Adult
Acris crepitans Travis County	90	72.2	44.4[1]	—	Young tadpole
Bufo compactilis	368	97.8	—	—	Tail bud
Gastrophryne olivacea	337	5.9	—	—	Blastula

[1] Includes some embryos that had not yet hatched but were very near to hatching at time counts were made.

[2] Does not include 16 embryos in tail bud stages at time counts were made.

they seldom climbed about on the sides of the aquarium and during the day they usually remained hidden beneath chips of bark on the aquarium floor.

♀ *Hyla versicolor* x ♂ *Acris crepitans.*—A few abnormal cleavages were noted in preblastula stages. Forty embryos had hatched or were very near to hatching by the fourth day after fertilization but none survived more than a few days after hatching. A. P. Blair (Moore, 1955) obtained embryos from this cross which survived to gastrulation or later.

INTERFAMILIAL CROSSES

♀ *Hyla versicolor* x ♂ *Bufo compactilis.*—All of the embryos showed abnormalities in early cleavage stages. All except 10 died before gastrulation and none hatched.

♀ *Hyla versicolor* x ♂ *Gastrophryne olivacea.*—Some abnormal cleavage occurred in all of the few that developed. All died before gastrulation.

The embryos of this and the preceding cross may have been haploids.

DISCUSSION AND SUMMARY

Results of the crosses agree in a general way with the commonly recognized systematic arrangement of the species concerned here. The only crosses (♀ *Hyla versicolor* x ♂ *Bufo compactilis* and ♀ *Hyla versicolor* x ♂ *Gastrophryne olivacea*) which failed to produce tadpoles involved species of different families (Bufonidae and Microhylidae, respectively). Within the family Hylidae, the intergeneric cross ♀ *Hyla versicolor* x ♂ *Acris crepitans* produced tadpoles, but none of these reached metamorphosis, whereas the cross ♀ *Hyla versicolor* x ♂ *Pseudacris clarki* produced six young frogs, at least two of which appeared to be mature at the time of death. Most authors agree that the phylogenetic relationship between *Pseudacris* and *Hyla* is very close and some doubt the validity of the genus *Pseudacris* as distinct from *Hyla* (Noble, 1931; Moore, 1955; W. F. Blair, 1959).

Mature offspring were obtained from two of the crosses within the genus *Hyla* (♀ *versicolor* x ♂ *baudini* and ♀ *versicolor* x ♂ *squirella*), while the other intrageneric cross (♀ *versicolor* x ♂ *cinerea*) produced tadpoles which failed to reach metamorphosis. We do not regard the latter as indicating distant relationship between the two parental species. It seems clear that the production of a viable adult F_1 demonstrates a considerable degree of genetic similarity, but the failure to do so does not necessarily indicate otherwise, particularly in the absence of any supporting evidence from other sources.

H. versicolor ranges over most of the eastern United States west to the Great Plains and is sympatric with the male parental species of two of the three hybrid combinations from which viable adults were obtained. *H. squirella* occurs in the coastal plain from southern Texas to Virginia; its range is included entirely within that of *H. versicolor* except in most of peninsular Florida where *versicolor* is absent. Both

species breed over relatively long periods in the spring and summer and they often utilize the same breeding sites. On several occasions we have observed mixed breeding congresses in southeastern Texas and southern Mississippi which included these two forms. The males were usually calling from the ground or from shrubs and small trees near shallow rain pools. Although neither geographical nor ecological isolation is complete, no natural *versicolor* x *squirella* hybrids have been reported. Other possible isolating mechanisms which may be functional in preventing hybridization between these two species are differences in size (*squirella* is smaller than *versicolor*), and breeding call. Basic differences in the calls of *squirella* and *versicolor* have been shown by the sound spectrograph analyses of W. F. Blair (1959).

Results of the laboratory crosses indicate little difference in viability between the controls and *versicolor* x *squirella* hybrids. However, the two hybrid males examined cytologically were sterile since they had evidently failed to produce sperm, and three other individuals lacked gonads altogether. It is possible that sterility among the hybrids was the result of inadequacies in laboratory technique, but this seems unlikely since the above mentioned sterile individuals possessed well-developed fat bodies and showed no other evidence of physical deficiency. The 15 controls possessed gonads of normal appearance and spermatogenesis was occurring in the testis of the male examined. We think it probable that if *versicolor* x *squirella* hybrids occur naturally, at least some will be sterile where *versicolor* is the female parent.

We were unable to test for fertility of the *versicolor* x *squirella* female hybrids, since none reached sexual maturity, but among the F_1 lot there was a disproportionately low number of females. Excluding the 11 individuals of uncertain sex, 34 of 42 frogs were males. Assuming the sexes to be of equal probability of occurrence, deviation from the expected 1:1 ratio is significant ($\chi^2=14.880$). There were also fewer females (five) than males among the 15 control frogs but deviation from an expected 1:1 ratio is not significant ($\chi^2=1.066$). If our assumption that the sexes should by chance occur in approximately equal numbers is correct, these data indicate that either fewer hybrid females than males were produced or that they were less viable than the hybrid males under laboratory conditions.

Pseudacris clarki is a grassland prairie species ranging from central Kansas through the middle portions of Oklahoma and Texas. Breeding occurs during or after rains from early spring through late summer. Grass-margined ponds and temporarily flooded fields are preferred breeding sites. Approximately the eastern one-third of the range of *P. clarki* is included within that of *H. versicolor,* however natural hybrids between the two are unknown. These species may occasionally use the same breeding sites at the same time, but differences in size (*clarki* is smaller than *versicolor*) and breeding behavior probably diminish the chances of cross matings. Although the males of both species may call from the ground near the breeding site, the call of *versicolor* is commonly uttered from shrubs or trees where the males may be perched 10 feet or more above the ground. Unlike *versicolor, clarki*

is not arboreal. Male *clarki* usually call while in the water holding to partially submerged vegetation, or from grass clumps in or very close to the water. To the human ear, the calls of the two species are very different.

In the laboratory crosses, relatively fewer *versicolor* x *clarki* hybrids survived through hatching and metamorphosis than controls, which probably indicates that the developing hybrids were less viable. At least two of the six hybrid frogs were without gonads at the time of death, but since they also lacked fat bodies, sterility may not have been the result of their hybrid origin. According to Noble (1931), the fat bodies are necessary for maintaining the health and normal development of the gonads.

Hyla baudini ranges from Honduras northward through Mexico and into extreme southern Texas, but fails to contact the range of *H. versicolor* by approximately 200 miles. In Texas, *versicolor* occurs as far south as Victoria in Victoria County and *baudini* is known from Cameron and Hidalgo Counties (Brown, 1950). Although we did not obtain a breeding test for fertility of the laboratory hybrids from the cross *H. versicolor* x *H. baudini,* the allopatric distribution of the parental species precludes any possible gene exchange between them at the present time. Survival of relatively fewer hybrids than controls through hatching and metamorphosis and the failure of one of three adult hybrids to produce gametes suggests that reproductive isolation has been at least partially established.

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Eleocharis, Subseries Palustres, in Illinois

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Recent Taxonomic Status

According to the latest monograph (Svenson, 1957), the genus *Eleocharis* is composed of eight series which are based mainly on morphological characteristics. In the past, the taxa belonging to the sixth series, Series Palustriformes, have been the subjects of many disputes due to the close similarities of the taxa within the series. The Series Palustriformes is composed of two subseries, Palustres and Truncatae. Six species are included in Subseries Palustres by Svenson: *Eleocharis kamtschatica, E. fallax, E. erythropoda* (*E. calva* of most authors), *E. halophila, E. macrostachya* (*E. mamillata* of some authors), and *E. smalli* (American *E. palustris* of some authors). Of these six species, three have been reported from Illinois—*E. erythropoda, E. macrostachya,* and *E. smalli.*

Approximately thirty years ago Fernald and Brackett (1929) conducted an extensive study on the Palustres complex. Of the three taxa cited by Svenson (1957), Fernald and Brackett had construed four species, namely *E. palustris* from Europe and North America, *E. smalli* from North America, *E. mamillata* from Europe and North America, and *E. calva* from eastern Asia, the Hawaiian Islands, and North America.

Later Svenson (1939) cited five species from this group, these being *E. palustris, E. smalli, E. calva, E. mamillata,* and *E. macrostachya,* of which *E. mamillata* was considered to be European and *E. macrostachya,* to be of the western United States.

Gilly (1946) with his work in Iowa recognized two species from Subseries Palustres—*E. calva* and *E. macrostachya.* He was unable to separate middle western plants with more acute scales and firm culms, usually identified as *E. smalli* by most workers, from the typical *E. smalli* because of a series of complex intergradations. He suggested that *E. smalli* might apparently belong to the Atlantic Coast region, and perhaps not readily separated from other species of the Palustres complex.

Fernald (1950) recognized four species of the Palustres group from North America: *E. palustris, E. smalli, E. macrostachya,* and *E. calva.* Jones (1950) also cited four species from this group in Illinois, recognizing the same ones that Fernald recognized, but replacing *E. macrostachya* with *E. mamillata.* Both Fernald and Jones used characters of the achene, fertile scales, and culms in their differentiation of the species.

Gleason (1952) recognized two species from North America, namely *E. palustris* and *E. calva. Eleocharis calva* is described as having a single large basal scale that completely encircles the culm, and

E. palustris, among other things, as having 2 or 3 basal scales. He also stated that *E. palustris* is usually segregated into three species: *E. smalli, E. palustris,* and *E. macrostachya,* each of which is variable and seems to be a phase of a single broad species.

Svenson (1957), in his latest monograph, recognized three species of this group from North America: *E. erythropoda* (replacing *E. calva*), *E. macrostachya,* and *E. smalli. Eleocharis smalli* is said to be the common *E. palustris of* New England with the European *E. palustris* apparently not being found in North America.

ANALYSIS OF CHARACTERS

Upon preliminary examination, the Illinois specimens of Subseries Palustres presented a problem in that they were difficult to classify into *E. erythropoda, E. smalli,* and *E. macrostachya.* As a result, a detailed study was made of all available specimens of Illinois material. The plant structures that showed the greatest possibilities of becoming major diagnostic structures were used in the detailed work. Such structures as stolons, sheaths, tubercles, and bristles were omitted from the study because of their variability and/or uniformity. The criteria used were the presence or absence of a single basal suborbicular scale that completely encircles the culm; culm thickness; spikelet shape and length, and color; and achene shape, length, and color. Each of these criteria will be discussed separately. A total of 203 Illinois specimens were carefully examined. The authors also had the opportunity to study several European and Western United States specimens deposited in the herbarium of the Missouri Botanical Garden.

Traditionally, *E. erythropoda* (*E. calva* of most authors) always has been described as having a single large suborbicular scale that completely encircles the culm. Svenson (1957) states that *E. macrostachya* may at times possess a single large suborbicular scale that completely encircles the culm. From modified scatter diagrams employed, it could be observed that the specimens with one basal scale appeared to be somewhat different in form as compared to the specimens with 2 or rarely 3 basal scales. Thus two large distinct categories were established: Group A having plants with one large suborbicular basal scale, and Group B having plants with 2 or rarely 3 basal scales.

Eleocharis erythropoda is described as having culms nearly filiform, 0.5-1.5 mm wide; *E. smalli* as having culms firm and wiry, 0.5-5.0 mm wide; and *E. macrostachya* as having culms filiform to 3.0 mm wide. Group A specimens possess culms ranging from 0.4-1.5 mm wide, averaging 0.6 mm, while the culms in Group B range from 0.6-2.7 mm wide, averaging 1.3 mm.

Eleocharis erythropoda supposedly has lanceolate spikelets 10-17 mm long; *E. smalli* has spikelets narrowly lanceolate, frequently becoming ovate and loosely-flowered in age, usually acute, and 5-20 mm long; and *E. macrostachya* has spikelets lanceolate (rarely ovate) and acuminate. Group A possesses spikelets that are ovate and acute, elliptic and acute, lanceolate and acute, or rarely lanceolate and acum-

inate with a cuspidate tip (6 specimens) 5-18 mm long, averaging 11 mm. Group B possessed spikelets that are ovate and acute, elliptic and acute, lanceolate and acute, lanceolate and acuminate, or lanceolate and acuminate with a cuspidate tip, 7-29 mm long, averaging 15 mm. Spikelet length and shape vary considerably in both groups. An individual specimen of either group may have three different forms of spikelets. This situation is especially common in Group B.

Eleocharis erythropoda is recorded as having brown fertile scales; *E. smalli* as having lanceolate fertile scales, pale to dark brown with rigid, acuminate, sometimes spreading tips; and *E. macrostachya* as having lanceolate fertile scales, firm, acute, scarcely hyaline at the apex and usually with a pale midrib and brown to black margins. The scales in Group A are ovate and obtuse to lanceolate and acute, the lowermost scales always ovate and obtuse with the uppermost scales lanceolate and acute, 1.1-3.7 mm long, averaging 2.8 mm, brown or straw-colored with a light midrib and hyaline margin. The scales in Group B are lanceolate and acute to lanceolate and acuminate, rarely ovate and obtuse, usually the lowermost scales of the spikelet lanceolate and acute or rarely ovate and obtuse and the uppermost scales lanceolate and acuminate, 2.7-4.5 mm long, averaging 3.4 mm, brown or straw-colored with a light midrib and hyaline margin. Only 5 specimens in Group B possess ovate and obtuse scales on the lower part of the spikelet. On these same specimens, the upper scales are lanceolate and acuminate (4 specimens) or lanceolate and acute (1 specimen). In all other respects these specimens are generally identical in form and appearance to the other specimens of Group B.

Eleocharis erythropoda achenes are described as being obovate, dark brown when mature, averaging 1.7 mm long (including the short, conic tubercle) and 1.0 mm wide; *E. smalli* achenes as being obovoid, averaging 2.0 mm long (excluding the depressed deltoid to elongate tubercle) and 1.1 mm wide, becoming dark brown in age; and *E. macrostachya* achenes as being obovate, glistening yellow when immature, becoming dark brown, averaging 1.8 mm long (not including the depressed deltoid to lanceolate tubercle) and 1.0 mm wide. Achenes of Group A are obovoid, 1.0-1.3 mm long, rarely 1.4-1.6 mm long (excluding the variable tubercle), yellow, becoming dark brown with age. Achenes of Group B are obovoid, 1.2-1.6 mm long, rarely 1.1 mm long (excluding the variable tubercle), yellow, becoming dark brown with age.

SUMMARY AND CONCLUSIONS

The authors feel that all specimens of Group A should be considered as one distinct species, and all specimens of Group B should be considered as a second distinct species for the following reasons: (1) Group A specimens with a large single basal suborbicular scale generally have thinner culms than Group B specimens which lack the large single basal suborbicular scale; (2) Group A specimens generally have shorter spikelets than Group B specimens; (3) Group A

specimens have scales that are usually smaller and predominantly ovate and obtuse to lanceolate and acute, while Group B specimens have scales that are generally larger and lanceolate and acute to lanceolate and acuminate. Achenes of Group A are identical to achenes of Group B as far as texture, color, and shape are concerned; however, the achenes of Group A are generally smaller than the achenes of Group B. The tubercles are essentially the same in both groups, being straw-colored or brown and short truncate to lanceolate and acuminate. The stolons, sheaths, and bristles are essentially the same in both groups.

The majority of the specimens in Group A have been determined previously as *E. calva,* and all of the Group A specimens fit Svenson's description of *E. erythropoda.* Svenson states that *E. macrostachya* may at times possess a single large suborbicular basal scale; however, all of our Group A specimens fall under the description of *E. erythropoda* rather than *E. macrostachya.*

The majority of Group B specimens were determined as *E. palustris, E. smalli, E. mamillata,* or *E. macrostachya.* Due to the intergrading characters, it is utterly impossible to separate individuals of Group B into different species or varieties. European specimens identified as *E. palustris* are essentially identical to Illinois specimens of Group B; however, the uppermost scales of the European *E. palustris* tend to be somewhat more lanceolate and acute, rather than lanceolate and acuminate. Variation in scale shape seems to be quite common as indicated by the five specimens of Group B that possess ovate and obtuse scales on the lower part of the spikelet. Specimens determined as *E. macrostachya* from Texas, Utah, and Missouri are essentially identical to Illinois Group B specimens. None of the examined *E. macrostachya* specimens possesses a single large suborbicular basal scale. It is recommended that all Group B specimens should be known as *E. palustris* as proposed by Gleason (1952).

As a result, the species of *Eleocharis,* Subseries Palustres, in Illinois, may be known as follows:

1. *Eleocharis erythropoda* Steud, Syn. Cyp. 76. 1855 [T: Ohio, Frank].

> *Scirpus glaucus* Torr. Fl. U.S. 44. 1824, non Lam. (1791).
> *Eleocharis calva* Torr. Fl. N.Y. 2:346. 1843, nomen provisiorum.
> *Eleocharis palustris* var. *calva* Gray, Man. 522. 1848.

Culms 0.4-1.5 mm wide, averaging 0.6 mm; spikelets ovate and acute, elliptic and acute, lanceolate and acute, or lanceolate and acuminate with a cuspidate tip, 5-18 mm long, averaging 11 mm, with a large single suborbicular basal scale completely encircling the culm; scales ovate and obtuse to lanceolate and acute, 1.1-3.7 mm long, averaging 2.8 mm, brown or straw-colored with a light midrib and hyaline margin; achenes obovoid, 1.0-1.3 mm long, rarely 1.4-1.6 mm long (excluding the tubercle), yellow, becoming dark brown with age.

2. *Eleocharis palustris* (L.) Roem. & Schultes, Syst. 2:151. 1817. [T: European].

Scirpus palustris L. Sp. Pl. 47. 1753.
Eleocharis calva of authors, non *E. calva* Torr. 1843.
Eleocharis mamillata of authors, non Lindb. f. 1902.
Eleocharis macrostachya Britt. ex Small, Fl. SE. U.S. 184. 1903.
Eleocharis smalli Britt. in Torreya 3:23. 1903.

Culms 0.6-2.7 mm wide, averaging 1.3 mm; spikelets ovate and acute, elliptic and acute, lanceolate and acute, or lanceolate and acuminate with a cuspidate tip, 7-29 mm long, averaging 15 mm, with 2 or rarely 3 basal scales; scales ovate and obtuse to lanceolate and acuminate, 2-7-4.5 mm long, averaging 3.4 mm, brown or straw-colored with a light midrib and hyaline margin; achenes obovoid, 1.2-1.6 mm long, rarely 1.1 mm long (excluding the tubercle), yellow becoming dark brown with age.

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The Subspecies of Cambarus diogenes

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Introduction

The aims of this research were (1) a taxonomic investigation of *Cambarus diogenes* and its subspecies, (2) a morphometric analysis of population variation, and (3) a presentation of distribution patterns and ecology of the subspecies.

Due to their burrowing habit, crawfish of this species are difficult to collect and no institution has a large series. Several major crawfish collections were examined. These included 1,206 preserved *C. diogenes* collected in many areas in the United States (Table I).

Girard (1852) first described *C. diogenes* from Washington, D. C. Subsequently, the species was recorded in Alabama, Arkansas, Colorado, Delaware, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Michigan, Mississippi, Missouri, Nebraska, New Jersey, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, West Virginia, Wisconsin, and Wyoming (Fig. 1). Williams and Leonard (1952) state that this range is one of the most extensive for any species of crawfish in the United States.

Variations of the species have been reported. Faxon (1898) described male form II specimens from Belmond, Iowa, differing from typical *C. diogenes* in having a long rostrum with a narrower, more tapering acumen. Ortmann (1906), analyzing Pennsylvania specimens, described differences between eastern and western forms on areola obliteration, rostrum and acumen shape, tuberculations on the chelae, and the proportionality of the chelae measurements. Rhoades (1944), in an analysis of Kentucky specimens, claimed to have found differences in eastern and western forms based on the degree of areola obliteration. Both Ortmann (*loc. cit.*) and Rhoades believed these to be intergrades. Ortmann also stated that Tennessee specimens were intergrades.

Faxon (1884) described a new variety (*ludoviciana*) from the New Orleans area based on the shape of the cephalothorax and rostrum. Since that time, *C. d. ludovicianus* has been reported also by Ortmann (1931) from Bolivar County, Mississippi, and Obion County, Tennessee.

One of the basic differences between the subspecies, particularly in the juvenile forms, is the color pattern of *C. d. ludovicianus*, which is discussed in a later section under "Color" in the description of the crawfish.

Ontogenetic variation has not been considered for this species and is discussed under the section "Statistical Analysis." Ecology and life history are also discussed under their respective sections.

Acknowledgments.—The author wishes to express his appreciation to the following persons and agencies for aid in obtaining specimens and in giving useful suggestions and criticisms: Dr. G. H. Penn, Tulane University, Tulane Collection; Dr. A. B. Leonard, University of Kansas Museum of Natural History Collection; Dr. E. Deichmann, Museum of Comparative Zoology Collection; Dr. F. A. Chace, Jr., Curator, United States National Museum Collection; F. A. Aldrich, Associate Curator of Limnology, Academy of Natural Sciences of Philadelphia Collection; J. J. Parodiz, Carnegie Museum Collection; and Dr. H. H. Hobbs, Jr., University of Virginia, personal collection.

TABLE I.—Specimen distribution according to states (♂I, male form I, sexually mature; ♂II, male form II, sexually immature; ♀, adult female, non-ovigerous; ♀e, adult female, ovigerous; j♂, juvenile males; j♀, juvenile females; all juveniles less than 15 mm cephalothorax length).

State	♂I	♂II	♀	♀e	j♂	j♀
C. d. ludovicianus						
Louisiana	8	9	33	3	124	77
C. d. diogenes						
Alabama	6	7	14	1	0	0
Arkansas	1	4	5	0	0	0
Colorado	6	0	8	0	0	1
Delaware	0	1	1	0	0	0
Florida	6	13	18	0	0	0
Georgia	2	8	9	1	2	0
Illinois	8	3	4	0	0	0
Indiana	43	2	16	0	0	1
Iowa	1	0	1	0	0	0
Kansas	4	6	15	4	0	0
Kentucky	4	8	16	3	0	2
Louisiana	6	18	30	0	34	59
Maryland	13	12	17	1	10	9
Michigan	18	7	15	0	0	0
Mississippi	2	8	32	0	2	1
Missouri	0	10	6	0	0	2
Nebraska	0	4	4	0	0	0
New Jersey	1	0	1	0	0	0
North Carolina	2	3	13	4	0	3
Ohio	7	8	8	1	1	3
Pennsylvania	39	47	93	3	0	8
South Carolina	1	0	1	0	0	0
Tennessee	7	13	20	1	1	5
Texas	0	1	1	0	0	4
Virginia	13	11	26	5	1	3
Washington, D. C.	1	0	2	1	0	0
West Virginia	2	1	5	0	0	0
Wisconsin	1	7	15	0	0	0
Wyoming	0	5	5	0	0	0
Total	202	216	434	28	175	179

METHODS AND MATERIALS

Measurements were made on adult and juvenile specimens. Juveniles (under 15 mm) were examined when a large series from a single female or a single locality was obtained. The source and number of specimens are included in Table II.

For the juvenile specimens, measurements were made of the lengths of the areola and cephalothorax. A ratio, cephalothorax length/areola length, was then calculated.

Not all measurements on adult specimens are shown on Figure 2. Measurements were cephalothorax length, cephalothorax width, rostrum width, distance between the postorbital spines, areola length, chela length, palm width, and dactyl length. In addition, antennal scale length, antennal scale width, pleopod length of male forms I and II, ischial spine length of the third pereiopod in male forms I and II, and annulus ventralis length and width in adult females were also measured. Ratios calculated were cephalothorax length/areola length, cephalothorax length/rostrum length, antennal scale length/width, cephalothorax length/ cephalic portion of cephalothorax length, cephalothorax length/width, cephalothorax

COLLECTION	JUV. ♂	JUV. ♀	♀♀	♂♂ I	♂♂ II	TOTAL
TU. C. D. D.	33	67	22	25	29	176
C. D. L.	124	77	27	7	7	242
C.M. C. D. D.		4	144	75	57	280
H.H.H. C. D. D.	6	10	88	30	49	183
A.N.S.P. C. D. D.		2	13	6	7	28
K.U.M.N.H. C. D. D.			21	4	10	35
U.S.N.M. C. D. D.	12	19	80	43	47	201
C. D. L.			5	1	2	8
M.C.Z. C. D. D.			33	11	8	52
C. D. L.			1			1
TOTAL	175	179	434	202	216	1206

TABLE II.—Age, sex and total number of specimens examined: *C.D.D.*, *Cambarus d. diogenes; C.D.L.*, *Cambarus d. ludovicianus*, TU., Tulane; C.M., Carnegie Museum; H.H.H., Hobbs; A.N.S.P., Acad. Nat. Sci. Phila.; K.U.M.N.H., Kansas Univ. Mus. Nat. Hist.; U.S.N.M., U. S. Nat. Mus.; and M.C.Z., Mus. Comp. Zool.

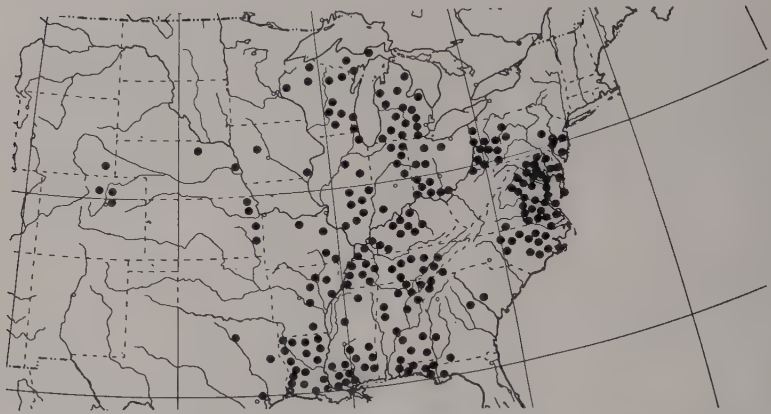

Fig. 1.—Distribution of *Cambarus diogenes diogenes* samples examined. Each dot represents a single county

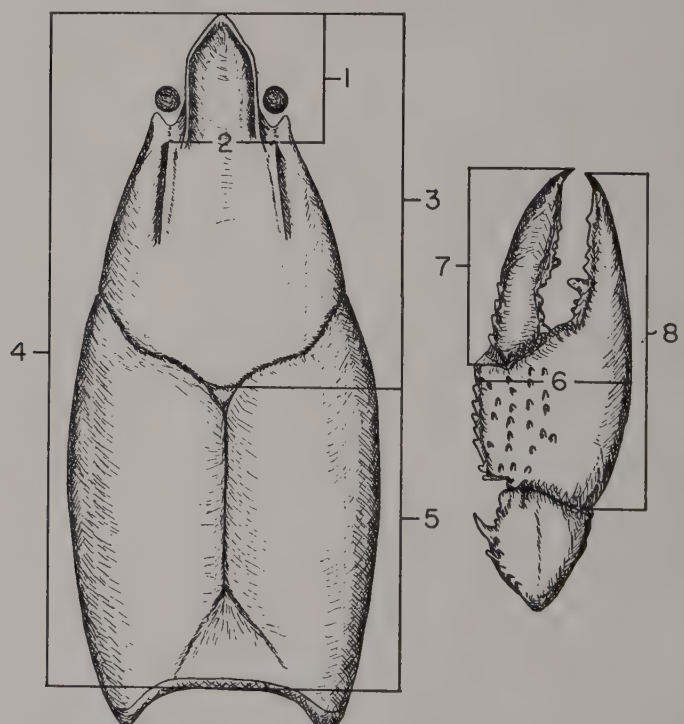

Fig. 2.—Standard crawfish measurements: 1—Rostrum length. 2.—Postorbital spine width. 3—Cephalic portion of cephalothorax length. 4—Cephalothorax length. 5—Areola length. 6—Palm width. 7—Dactyl length. 8—Chela length.

length/ chela length, chela length/rostrum length, rostrum length/ width, chela length/palm width, and chela length/dactyl length.

For clarification of data and for discussion of problems concerning the subspecies of *C. diogenes,* the data have been divided according to river drainages (Fig. 3). The specimens from the various collections are designated as follows: male form I (♂I), male form II (♂II), adult females (♀), females with eggs (♀e), juvenile females (j♀), and juvenile males (j♂).

In the section on "Statistical Analysis," Student's *t* test was applied to discern the significance of differences between means of various samples. Except for a large series from Mississippi, mean values are considered significantly different at the 5 percent level of confidence ($t = 1.67$). Comparisons were made between the mean value for a single drainage and that for the entire sample of *C. d. diogenes.* In the case of the one large drainage area from Mississippi, the test is used for comparison of this individual lot with specimens from the rest of the Mississippi drainage.

The major drainage areas are as follows: Mississippi River, Sabine River, Chattahoochee River, Missouri River, North Platte River, Delaware River, Ohio River, Tennessee River, Pearl River, Atlantic Coast Drainage (exclusive of Potomac River), Potomac River, Great Lakes Drainage, Wabash River, Red River, and the Alabama River. The drainage area for *C. d. ludovicianus* is treated separately.

ACCOUNTS OF SUBSPECIES

Cambarus diogenes diogenes Girard

C. d. diogenes has been adequately described by zoologists. For

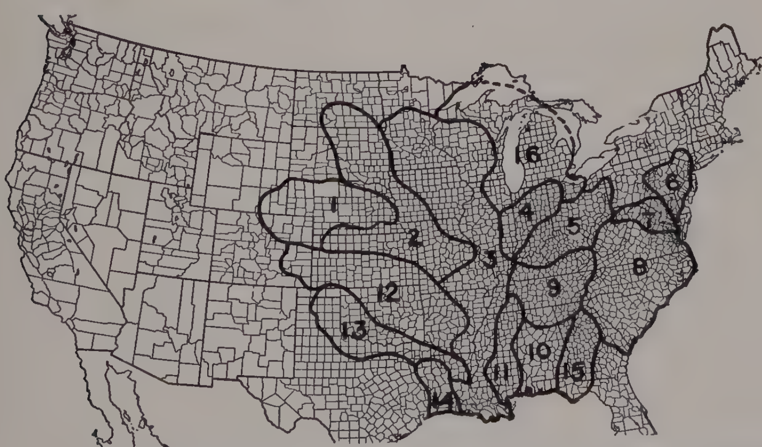

Fig. 3.—Major river drainages: 1—North Platte. 2—Missouri. 3—Mississippi. 4—Wabash. 5—Ohio. 6.—Delaware. 7—Potomac. 8—Mid-Atlantic. 9—Tennessee. 10—Alabama. 11—Pearl. 12—Arkansas. 13—Sabine. 14—Red. 15—Chattahoochee. 16—Great Lakes.

the most recent description, I refer the reader to Williams and Leonard (1952) and add here only the new material produced by the present investigation.

Synonymy.—*Cambarus diogenes* Girard, 1852, Proc. Acad. Nat. Sci. Phila., 6:88; *Cambarus nebrascensis* Girard, 1852, Proc. Acad. Nat. Sci. Phila., 6:91; *Cambarus obesus* Hagen, 1870, Illus Cat. Mus. Comp. Zool., 3:81; *Cambarus dubius* Osborn and Williamson, 1898, Ann. Rept. Ohio State Acad. Sci., 6:21 (non *dubius* Faxon); *Cambarus* (*Bartonius*) *diogenes* Girard, Ortmann, 1905, Proc. Amer. Philos. Soc., 44:120; *Cambarus diogenes diogenes* Girard, Hobbs, 1942, Am. Midl. Nat., 28(2):334.

Type locality is Washington, D. C., with the type specimens unknown; paratype in collection of the Academy of Natural Sciences in Philadelphia according to Faxon (1914).

Diagnosis.—Cephalic portion of cephalothorax length/areola length ratio always more than 1.40 (mean 1.49); cephalothorax length/areola length 2.49; areola obliterated; antennal scale length/width less than 1.45.

Male form I. Areola length 41 percent of entire length of cephalothorax. Antennal scale length/width less than 1.45.

Female. Annulus ventralis 1.4 times as wide as long.

Color.—An over-all dark-colored crawfish. The ground color of the dorsal surface shades from olive-green to brown; the ventral surface is entirely cream colored. The chelae shade from olive-green at the base of the finger to creamy buff at the apices, with both fingers tipped in red. The joints of the pereiopods are reddish brown. Young specimens are mostly green, with the older specimens mostly dark brown. This color pattern of the adult is universally agreed upon by zoologists.

Color varies greatly among the members of this subspecies. The coloration may be due to the chemical composition of the soil in which these animals live.

Ortmann (1905), writing about Pennsylvania specimens, stated that the ground color was brownish or olive-green in the eastern portion of the state, with purple-brown ground color in the western portion of the state. The rest of the coloration of the eastern form closely resembles the descriptions of other zoologists. In western Pennsylvania, a verdigris green is present at the base of the fingers, the chelae are orange-red tipped, with the rostrum having a reddish margin. A dull red ground color has also been reported in this area.

Hobbs and Marchand (1943) reported two color variations, a solid color phase and a striped phase, of this subspecies from the Reelfoot Lake area. The striped phase has an olive-green ground color, with the margins of the rostrum and cervical groove having a reddish cast. The thoracic region has a whitish-tan mid-dorsal stripe and the abdomen has three longitudinal stripes of the same color. These abdominal stripes have also been seen by me in preserved specimens from Mississippi. The telson and uropods have pinkish-

red borders, with the median portions iridescent green. The chelae are tipped in red and the pereiopod joints are reddish.

The solid phase has an olive-green ground color with an unmarked cephalothorax. The posterior margins of the abdominal segments are outlined with a thin red band, while the margins of the uropods and telson are red. The ridges of articulation of the chelae are red.

Specimens from Hobbs' collection from South Carolina and northern Georgia show a ground color of dull purple with the ventral surface cream to golden. This color persists on the articulation surface of the chelae with the tips of the fingers red. Joints are also red, and no abdominal stripes have been found.

Turner (1926), in Ohio specimens, found the ground color brownish-green, the ventral surface buff to cream, the cephalothorax reddish at the margins, and the tips of the claws red.

Faxon (1885), in Washington, D. C. specimens, described the basic ground color as olive, with the ventral surface cream. The margins of the rostrum are red as well as the margins of the postorbital ridges and the margins of the abdominal segments. The chelae are cream colored within, with reddish fingers tipped in red.

Pearse (1909) gave the ground color as brown. The margins of the rostrum and posterior borders of the abdominal segments red. The chelae are greenish and brown with the outer margins bordered in white.

Hobbs collected two specimens with additional color variations and supplied his notes on them. These were examined and subsequently diagnosed by the author as *C. d. diogenes.* The color patterns, however, are distinct from any so far reported. The first specimen (HHH 4-1258-9b, Gordon Co., Georgia) shows the rostrum outlined in orange, with the dorsal surface of the cephalothorax and abdomen a pinkish-gray. The entire ventral surface is pinkish-cream. The abdominal segments are tipped in pinkish-cream with the posterior margins of the segments lined in pinkish-gray. The palm of the chela is black on the dorsal medial surface with white tubercles; the dorsolateral surface is pale orange; the ventral surface is entirely cream. The area adjacent to the movable finger is pinkish-orange. The chelae are tipped in pinkish-orange. The legs are entirely cream.

The second specimen (HHH 4-1358-8, Cherokee Co., Alabama) has a ground color of lavender-gray. The tips of the abdominal segments are pinkish-cream as well as the posterior margins of the segments. The lateral uropod segments are the same color on the margins. The ventral surface is entirely cream. The palm is black on the medial surface with white tubercles. The lateral margin is orange. The distal half of the immovable finger and the distal third of the dactyl are scarlet. The margins of the rostrum are outlined in a pinkish color.

The majority of the specimens of *C. c. diogenes* examined were

of the solid colored phase as described by Hobbs and Marchand (1943).

The foregoing description tends to emphasize the following points: (1) *C. d. diogenes* coloration and striping varies from section to section of its range, with no single color pattern being localized in one particular drainage, and (2) the solid color phase is the most typical coloration of *C. d. diogenes* occurring in all sections of its range.

Cambarus diogenes ludovicianus Faxon

Synonymy.—*Cambarus diogenes* Girard (in part), 1852, Proc. Acad. Nat. Sci. Phila., 6:88; *Cambarus obesus* Hagen (in part), 1870, Illus. Cat. Mus. Comp. Zool., 3:81; *Cambarus diogenes* var. *ludoviciana* Faxon, 1884, Proc. Amer. Acad. Arts and Sci., 20:144; *Cambarus diogenes* Girard (in part), Shufeldt, 1896, The Observer, 7:85.

Type locality of this subspecies is New Orleans, Louisiana; co-type specimens are deposited in the United States National Museum (*USNM* 5625 and 5504).

Diagnosis.—Ratio of cephalic portion of cephalothorax length/areola length always less than 1.30 (mean 1.24); sides of cephalothorax more or less parallel, or slightly ovate; cephalothorax length/areola length 2.24; areola obliterated; rostrum narrow; antennal scale length/width greater than 1.45; sides of antennal scale nearly straight or parallel. Annulus ventralis as long as wide with fossa on right side; sinus originating on right side, then turning medially to midline and from there continuing posteriorly on midline.

Description.—Male form I. Body narrow with sides nearly parallel or slightly ovate; abdomen only slightly wider than cephalic portion of cephalothorax; greatest width of thorax about halfway caudad between cephalic groove and end of thoracic portion.

Areola obliterated; cephalic portion of cephalothorax 1.24 times as long as areola; areola length about 45 percent of entire length of cephalothorax.

Rostrum directed slightly cephaloventrad; upper surface is deeply excavated; no spines, rostrum curves gently into acumen which ends in a slight spinous structure, hence, it is not set off. Margins of rostrum glabrous, one row of punctulations on rostral border, central portion glabrous; rostral ridges inflated. Postorbital spines low and terminating anteriorly without spines. Branchiostegal spines blunt, minute.

Cephalothorax surface punctate dorsally and granulate laterally.

Cephalic portion of telson with one spine on each caudoventral corner.

Epistome wider than long, ending bluntly anteriorly.

Eyes normal.

Antennules normal. No spine on any segment.

Antennae extend to second or third abdominal segment. Antennal scale long, extending to or just anterior to the tip of the rostrum;

antennal scale length/width 1.49; nearly uniform width with sides nearly parallel. Antennal scale more or less rectangular; strong spine on anterior lateral end; heavily filamented on medial border.

Right chela not depressed; palm inflated, bearing no spines; fingers recurved slightly ventrally from their bases; fingers heavily punctate dorsally and ventrally; no granulations are apparent. Immovable finger with one large tubercle on basal third of opposable surface; rest of surface with small tubercles. Movable finger with no large tubercles on opposable surface. Entire surface covered with moderate sized tubercles. Opposable surface meets along anterior one-half but widely separated along posterior one-half.

Carpus longer than wide, being longest on central position; well defined dorsal longitudinal groove. Three well-defined spines on mesial surface and one large ventral spine. Two large tubercles on dorsal and ventral surfaces at base of movable finger.

Meropodite of first pereiopod with two prominent spines anteriorly and dorsally.

Hook present on ischiopodite of third pereiopod only. Hook is simple and curved medially.

First pleopod extends to caudal margin of coxopodite of third pereiopod when abdomen is flexed, terminating in two prominent parts. Parts bent at 90° angle to shaft of pleopod. Central projection corneous and blade-like; recurved caudomesiad; fusion line clearly defined. Mesial process bulbous and ending in a nipple-like projection. Lateral margin of endopodite is heavily bearded.

Male form II. Similar to male I. Acumen more distinctly separated from rostrum. Pleopods non-corneous and slightly recurved with less bearded lateral margin of endopodite. Hook of third ischiopodites absent or greatly reduced. Chelae reduced.

Female. Similar to male form I. No hook on ischiopodites of third pereiopods. Annulus ventralis immovable, approximately as long as wide. Sinus depression on right side, turning medially at posterior end of depression until reaching midline, then proceeding caudally to posterior margin of annulus. Sternites of fourth and fifth thoracic segments are smooth and do not encroach on the annulus. The center of the depression appears scooped out, no knobs evident.

Color.—*C. d. ludovicianus* has a uniform coloration, with the juveniles showing the most brilliant coloration. The basic color is a brilliant blue with the ventral surface entirely cream. The abdomen has three longitudinal red stripes, with the base of the telson and uropods marked in red, as well as the margins of the uropods but not the telson. The first pereiopod is a light blue, with the second through the fifth pereiopods being cream colored. Fingers of the chelae are tipped in red. Joints of pereiopods are red.

In the adult, usually only three longitudinal abdominal stripes of light red or orange persists, against a slightly blue background.

Color pattern for this subspecies is diagnostic and is exemplified best in the juvenile form.

STATISTICAL ANALYSIS

Specimens were divided into four categories: (1) juveniles (under 15 mm cephalothorax length), (2) male form I, (3) male form II, and (4) adult females (including ovigerous and non-ovigerous individuals).

Specimens were grouped geographically according to the major river drainages for simplification of handling the data. The river drainages are listed below in west to east, north to south sequence: North Platte, Missouri, Red, Sabine, Arkansas, Mississippi, Great Lakes, Wabash, Ohio, Tennesee, Pearl, Alabama, Chattahoochee, Delaware, Potomac, and Mid-Atlantic. No specimens were examined from the Arkansas drainage. The distribution of *Cambarus d. ludovicianus,* although including drainage into the Gulf of Mexico and the lower Mississippi River, is referred to as the Alluvial Fault Basin (Fig. 4).

Line graphs are employed for pictorial representation of data (cf. Cazier and Bacon, 1949). Of the ratios calculated and graphed, the variation of all but one was so great as to be virtually useless. *C. d. diogenes* ratios are as follows: cephalothorax length/chela length, range 0.92-2.05, mean 1.33-1.50; rostrum length/width, range 0.93-2.04, mean 1.27-1.50; cephalothorax length/width, range 1.39-2.72, mean 2.06-2.29; chela length/dactyl length, range 1.27-2.34, mean 1.56-1.70; chela length/palm width, range 1.70-2.74, mean 2.08-2.28. The above values overlap those for *C. d. ludovicianus* and are considered of little value for this statistical analysis. Only the cephalic portion of the cephalothorax length/areola length ratio does not show the overlap in values.

Geographical variation.—In the differentiation of the subspecies of *C. diogenes,* the one useful ratio is that of cephalic portion of cephalothorax length to areola length. Visual inspection of the plot of mean values for this ratio for all *C. d. diogenes* samples indicates

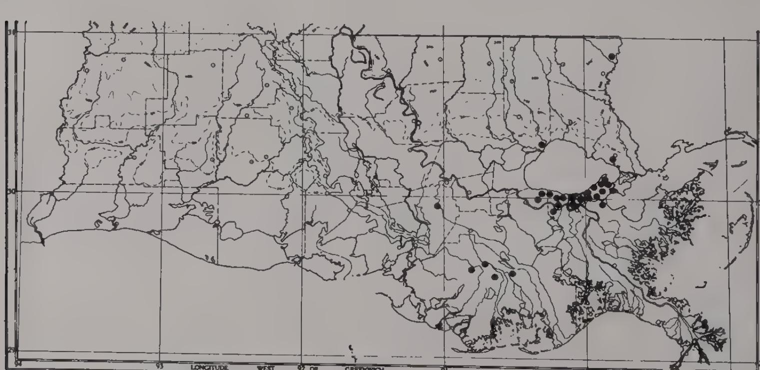

Fig. 4.—Distribution of *Cambarus diogenes ludovicianus.* Each dot represents one sample examined

that the range varies from 1.41 to 1.48, excepting those of the Sabine and Wabash drainages (Fig. 5). When the Student's t is employed to determine the significance of difference between the mean value (1.44) for the entire sample of *C. d. diogenes* and that of each drainage, two additional samples, the Mid-Atlantic and Red River drainages are found to vary significantly at the 5 percent level.

The small mean (1.36) for the Wabash drainage is attributed to 35 specimens from Wells Co., Indiana. The mean of the Wells Co. group is 1.33 (range 1.17-1.81, SD 0.14, SE 0.02). The 14 other specimens from this drainage have a mean of 1.43 (SD 0.10, SE 0.02) which is equal to that of the mean of the entire *C. d. diogenes* sample. I cannot explain the low value for the Wells Co. group. The Wabash River in Wells Co., Indiana, cuts diagonally across the county in a southwesterly direction. The county is 850 feet above high tide

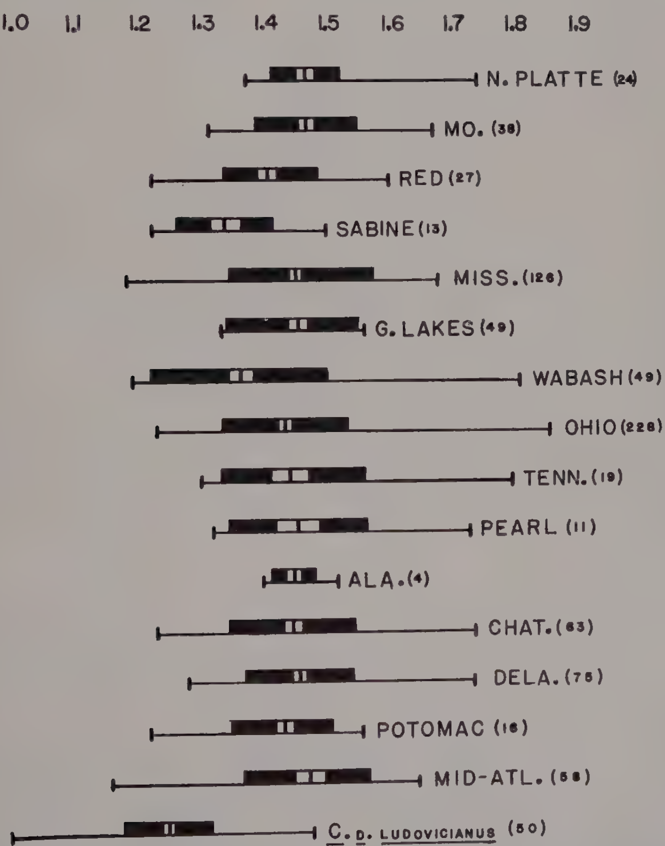

Fig. 5.—Comparison of cephalic portion of cephalothorax length/areola length ratios by river drainages for *C. d. diogenes*. *C. d. ludovicianus* included.

level, is not surrounded by mountains, and is not geographically isolated from the surrounding area or the rest of the Wabash drainage. The river originates a short distance to the southeast in Ohio. Samples from the headwaters of the drainage are not available. Examination of specimens from this region is required to determine the exact status of the population. Perhaps some type of isolation has occurred, as in Colorado and Wyoming, and subspeciation is in progress at the headwaters of the Wabash drainage. It should be emphasized that the only difference between Wells Co. individuals and those from other areas is in the value of the ratio. Other morphological features and all other statistics fall within the normal variation of *C. d. diogenes.*

The low mean value, 1.34, for the small (13 individuals) Sabine drainage sample was first attributed to sample size. However, the difference between the mean of all *C. d. diogenes* samples and that of the Sabine drainge is significant ($t = 4.80$) and the population deserves further investigation. Similar remarks may be made for the sample from the Red drainage. The mean value for 27 individuals is 1.39 and this is significantly different from that of the entire sample.

The mean value for the Mid-Atlantic drainage is 1.48. Mention has been made of Ortmann's (1906) and Rhoades' (1944) eastern and western varieties. The significant deviation in mean value of the ratio for the Mid-Atlantic sample, plus the areola gap in the western form, indicates definite geographic variation. Isolation of the Mid-Atlantic drainage by the Appalachian and Allegheny Mountains is of considerable significance in accounting for this variation.

From east to west the ratio of the cephalic portion of the cephalothorax length to areola length becomes progressively larger, with the largest ratios (i.e., shortest areolas) occurring in Colorado and Wyoming (1.45 and 1.47 respectively). Size of the crawfish also becomes larger the further one progresses westward (up to 65 mm cephalothorax weight). Also to be noted is that the areola is shorter in northern specimens and becomes progressively longer as one proceeds southward.

The areola, then, steadily increases from east to west, north to south.

Examination of this particular ratio in *C. d. ludovicianus* specimens (50) shows a mean of 1.24, considerably lower than for *C. d. diogenes.* This ratio is used as one of the major differentiation points between the two subspecies.

Ortmann (1906) reported that *C. d. ludovicianus* was also found in Reelfoot Lake, Obion Co., Tennessee. Examination of specimens from this area (23) showed that the mean value of the cephalic portion of the cephalothorax length to areola length ratio is 1.43 (SD 0.13, SE 0.03). The soil of Reelfoot Lake area is not that of the Alluvial Fault Basin as found in Louisiana and apparently *C. d. ludovicianus* is limited to the Basin in Louisiana. The high mean

value for these specimens, the absence of the typical color pattern of the juveniles and adults, the greater width/length ratio of the annulus ventralis (1.49:1), and the range of these individuals places this population in the *C. d. diogenes* group. There is no evidence to conclude that a new subspecies is developing in this area. All ratios, color patterns and physical evidence refute the designation of this population as *C. d. ludovicianus*.

Ontogenetic variation.—Since the number of juveniles from each drainage is small, only the data from an eastern drainage and that from a western drainage (affording the largest number of specimens) were used.

These examples are found in Figures 6, 7 and 8. The Mississippi drainage, extending from Wisconsin to the Gulf of Mexico, covers the largest drainage area. It is not necessary to divide the drainage into upper and lower fractions as the mean values from these two

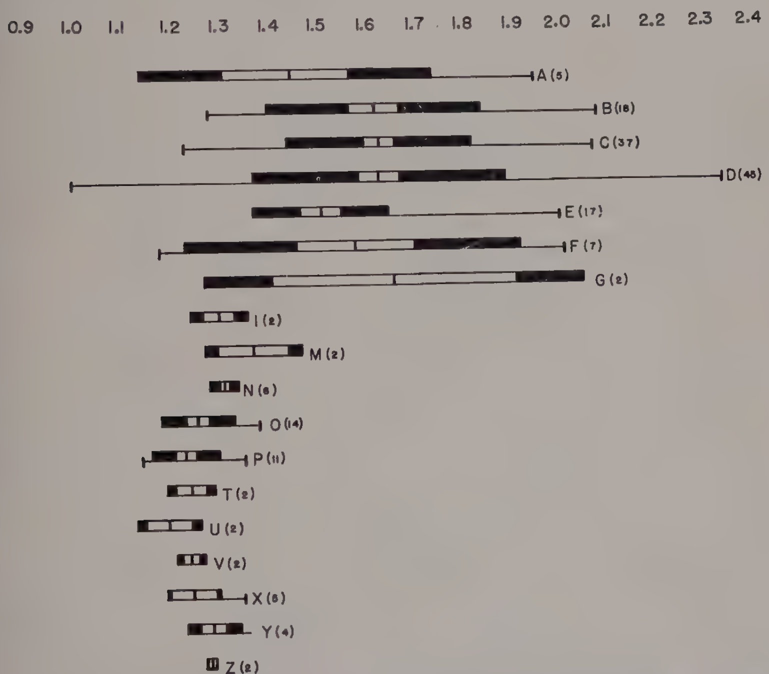

Fig. 6.—Ontogenetic and sexual variation in cephalic portion of cephalothorax length/areola length ratio for *C. d. ludovicianus*. Adult specimens are grouped according to sex and cephalothorax length (M-Z). Juvenile specimens are grouped according to cephalothorax length (A-I). All measurements are in mm. *Juveniles:* A. 5-5.9; B. 6-6.9; C. 7-7.9; D. 8-8.9; E. 9-9.9; F. 10-10.9; G. 11-11.9 and I. 13-13.9. *Adult females:* M. 25-29.9; N. 30-34.9; O. 35-39.9; and P. above 40. *Male form I:* T. 30-34.9; U. 35-39 9; and V. above 40. *Male form II:* X. 20-24.9; Y. 25-29.9; and Z. 30-34.9.

areas are almost identical (upper —1.46, lower — 1.44, combine — 1.45).

Juveniles, male forms I and II, and females were grouped accord ing to cephalothorax length into the following categories: juvenile cephalothorax length in mm, 5-5.9, 6-6.9, 7-7.9, 8-8.9, 9-9.9, 10-10.9 11-11.9, 12-12.9, 13-13.9, 14-14.9; male forms I and II, and female 15-19.9, 20-24.9, 25-29.9, 30-34.9, 35-39.9, and over 40. The ratio were averaged for each.

No male form I crawfish are found under 30 mm cephalothora length. Male form II have been found to occur up to 45 mm i cephalothorax length.

Ontogenetic variation in the cephalothorax length/areola lengt ratio is most noticeable among juvenile *C. d. ludovicianus* (Fig. 6) The smaller cephalothorax length, the larger the ratio, with th

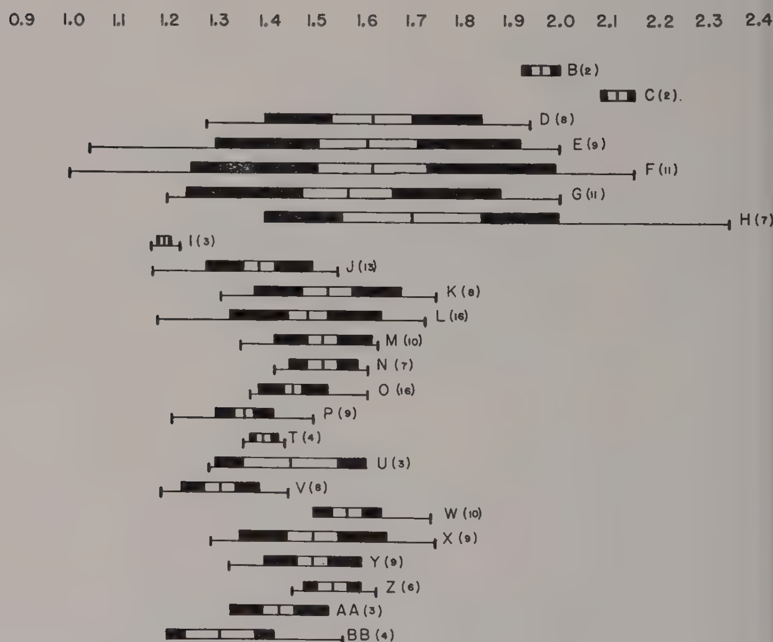

Fig. 7.—Ontogenetic and sexual variation in cephalic portion of cephalothorax length/areola length ratio for *C. d. diogenes* in the Mississippi drainage. Adults grouped according to sex and cephalothorax length (K-BB). Juveniles grouped in cephalothorax length only (B-J). All measurements in mm. Juveniles: B. 6-6.9; C. 7-7.9; D. 8-8.9; E. 9-9.9; F. 10-10.9; G. 11-11.9; H. 12-12.9; I. 13-13.9; and J. 14-14.9. *Adult females:* K. 15-19.9; L. 20-24.9; M. 25-29.9; N. 30-34.9; O. 35-39.9 and P. above 40. *Male form I:* T. 30-34.9; U. 35-39.9; and V. above 40. *Male form II:* W. 15-19.9; X. 20-24.9; Y. 25-29.9; Z. 30-34.9; A.A. 35-39.9; and BB. above 40.

smallest ratio occurring in the 13-14 mm group (1.30). A downward progression is found from a mean of 1.63 to 1.30.

The largest mean value of the adults is 1.37. Apparently after ecdysis from juvenile to adult, the largest ratio is reached, which progressively becomes smaller until the minimum ratio of the adult is obtained (1.24).

In *C. d. ludovicianus,* form II males have a retrograde ratio, with the ratio slowly enlarging until the maximum for form I males is reached. At the maturation change from form II to form I, the ratio again becomes smaller until the minimum mean is reached (1.21). At this point, no further diminution of the ratio is found.

The Mississippi specimens seem to show the best correlation (Fig. 7). The ratio of the juveniles gradually declines until adulthood is reached. For form II males and for females, the ratio steadily declines until the minimum value is obtained. As form II males reach maturity and molt, the largest ratio of form I males is attained. The ratio again declines until the minimum value is obtained.

Ontogenetic variation has been worked out for the Delaware specimens (Fig. 8), with the same ratio decline being evidenced from juveniles to adults.

Therefore, an ontogenetic change in the ratio of cephalic portion of the cephalothorax length/areola length occurs in *C. d. diogenes*

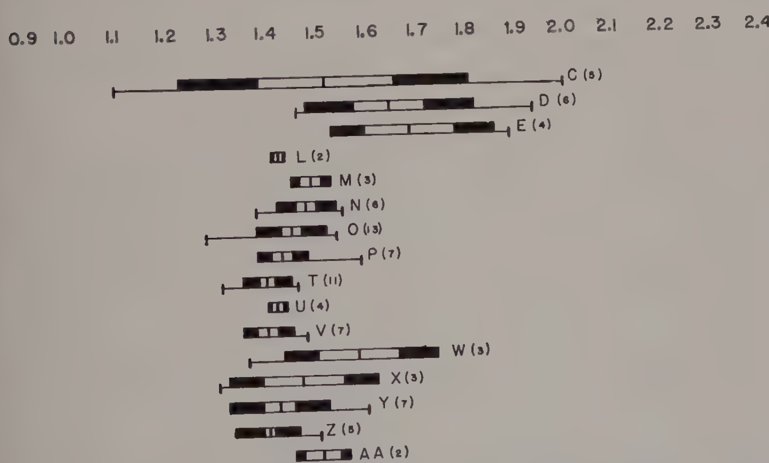

Fig. 8.—Ontogenetic and sexual variation in cephalic portion of cephalothorax length/areola length ratio for *C. d. diogenes* in the Delaware drainage. Adults grouped according to sex and cephalothorax length (L-AA). Juveniles grouped according to cephalothorax length only (C-E). All measurements in mm. *Juveniles:* C. 7-7.9; D. 8-8.9; and E. 9-9.9. *Adult females:* L. 20-24.9; M. 25-29.9; N. 30-34.9; O. 35-39.9; and P. above 40. *Male form I:* T. 30-34.9; U. 35-39.9; and V. above 40. *Male form II:* W. 15-19.9; X. 20-24.9; Y. 25-29.9; Z. 30-34.9; and AA. 35-39.9.

in that the ratio gradually decreases from the juveniles to the adult. This decrease is also evidenced in *C. d. ludovicianus* specimens.

LIFE HISTORY

Specimens have been examined from the range of *Cambarus diogenes diogenes* in the United States from every month of the year. Males of form I have been examined from every month except January, and the greatest numbers are found in April and September (Table III).

Bundy (1877) reported ovigerous females in Indiana on January 1, 1876. Tarr (1884) reported ovigerous females in the vicinity of Washington, D. C., in May. Ortmann (1906), in Pennsylvania, found copulation and hatching occurring in April, May and early June, with no form I males occurring until late June and July. In Wisconsin, Graenicher (1913) reported the occurrence of ovigerous females from late March to the middle of May. Hay (1918) in Indiana, found copulation occurring on April 4 and eggs present by April 17, indicating a two-week period between copulation and egg extrusion for this subspecies of crawfish. Creaser (1930) also found Michigan females with young occurring from April to June. Creaser (1932) found Indiana females with young in April and Michigan females in June.

Specimens examined by the author included ovigerous females in March (1), April (19), May (17), and October (1). The last was taken in Maryland. Females with young have been found in April and May.

All available evidence indicates that egg laying occurs in late

	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.	TOT.
♂ I		3 / .3	15 / 1.5	52 / 5.2	15 / 1.5	7 / .7	5 / .5	15 / 1.5	22 / 2.2	5 / .5	6 / .6	5 / .5	150 / 15
♂ II		5 / .5	6 / .6	18 / 1.8	26 / 2.6	22 / 2.2	25 / 2.5	41 / 4.2	29 / 2.9	8 / .8	10 / 1	8 / .8	198 / 19.9
♀ L		3 / .3	26 / 2.6	75 / 7.6	71 / 7.1	41 / 4.2	31 / 3.2	72 / 7.2	45 / 4.6	15 / 1.5	5 / .5	3 / .3	387 / 39.1
♀ EGGS			1 / .1	19 / 1.9	17 / 1.8					1 / .1			38 / 3.9
♀ YOUNG				2 / .2	2 / .2								4 / .4
♂ JUV.				13 / 1.4	9 / .9	15 / 1.5	10 / 1	13 / 1.4	2 / .2	1 / .1	2 / .2	1 / .1	66 / 6.7
♀ JUV.			3 / .3	22 / 2.2	24 / 2.5	60 / 6	14 / 1.4	19 / 1.9	4 / .4	1 / .1	2 / .2		149 / 15
TOT.	0	11 / 1.1	51 / 5.1	201 / 20.3	164 / 16.6	145 / 14.6	85 / 8.6	160 / 16.1	102 / 10.3	31 / 3.1	25 / 2.5	17 / 1.7	992 / 100

TABLE III.—Seasonal distribution of specimens of *Cambarus d. diogenes* examined, segregated according to age and sex (in each square, the upper triangle represents number of specimens; lower triangle represents percentage).

March, April and May, with the young hatching in April, May and June. Only the Indiana record of Bundy of ovigerous females in January is an exception to the above. The October and January occurrences cannot be discounted, but indicate that copulation occurs at two times of the year — in late autumn (October and November) and in the early spring (March, April and May). This surmise is supported by the data collected by the author.

Even though copulation occurred in October and November, there is only one record of an ovigerous female in that period (Bundy, 1877).

There appears to be a definite increase in the number of juveniles after May (Table II, June — 75, July — 24, August — 32). The greatest number of juveniles occurred from April through July, indicating that copulation occurs in late March through May.

The absence of juveniles in December through the middle of March seems to refute the thought that copulation occurs twice a year. Only the single October ovigerous female supports the idea of semi-annual copulation. Whether this single specimen was alive at the time of capture was not recorded. If alive, it is extremely doubtful that the eggs would have hatched before spring in Maryland. The developmental state of the eggs could not be determined in the preserved specimen.

The *C. d. ludovicianus* specimens are few but revealing in the character of their seasonal distribution (Table IV). Ovigerous females were found only in December (1) and January (2). Juveniles have been found in March and April, with the greatest abundance in March. Since the range of *C. d. ludovicianus* is character-

	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.	TOT.
♂ I		1 / .55	1 / .55		1 / .55		1 / .55	1 / .55	1 / .55				6 / 3.3
♂ II			5 / 2.8	2 / 1.1			3 / 1.6			1 / .55			11 / 6.2
♀		1 / .55	17 / 9.2	4 / 2.2	2 / 1.1		4 / 2.2			1 / .55	1 / .55		30 / 16.4
♀ EGGS	2 / 1.1											1 / .55	3 / 1.7
♀ YOUNG													0
♂ JUV.			69 / 37.1	4 / 2.2									73 / 39.3
♀ JUV.			45 / 24.4	16 / 8.7									61 / 33.1
TOT.	2 / 1.1	2 / 1.1	137 / 74.1	26 / 14.3	3 / 1.7	0	8 / 4.4	1 / .55	1 / .55	2 / 1.1	1 / .55	1 / .55	184 / 100

TABLE IV.—Seasonal distribution of specimens of *Cambarus d. ludovicianus* examined, segregated according to age and sex (explanation as in Table III).

ized by a relatively temperate climate, it is safe to say that copulation occurs in December and January, with hatching in March and April.

Climatic conditions in the New Orleans area in December and January (mean temperature 55° F) are closely allied to those of the northern section of the country in March and April (mean temperature 53° F). Hatching temperatures for the two subspecies are also closely allied, as the March and April mean temperatures (65° F) in New Orleans area are similar to April, May and June temperatures (62° F) in the northern section of the range.

It is tentatively concluded, then, that copulation in *C. d. diogenes* occurs twice a year: (1) late autumn — October and November, and (2) early spring — March, April and May. The eggs hatch in April through July. For *C. d. ludovicianus,* copulation occurs once a year (December and January) with young hatching in March through May.

A large series of specimens needs to be collected from the northern range of *C. d. diogenes* with particular emphasis on the appearance of the juveniles and the females with eggs.

Copulation may occur only once a year for *C. d. diogenes* but present evidence does not support this premise.

ECOLOGY

Burrows.—Individuals of all ages of *Cambarus diogenes* are burrowers of great efficiency, probably more adept in this habit than any other crawfish. For this reason, much time has been devoted to the observation of the burrows of this animal. The ecology of *C. d. diogenes* has been extensively investigated, and for this reason, only a brief summary is given here. Girard (1852) made extensive investigations of *C. d. diogenes* burrows around Washington, D. C. Of them he wrote:

> The holes, as they appear at the surface of the ground, are nearly circular, from seven-tenths of an inch to an inch and a half in diameter. The depths of the burrow varies according to the locations; this we generally found to be from sixteen inches to two feet, and sometimes three feet or more. The construction of the burrow itself is often exceedingly simple; from the surface of the ground the excavation exhibits a gradual slope in direction, more or less undulating for a distance of from five to ten inches, when it becomes vertical for six or eight inches, and then terminates in a sudden, bottle-shaped enlargement, in which the animal is found, the bottom of the burrow having no subterranean communication, no other issue except towards the surface; it is entirely isolated from its neighbors and leaves no chance for escape to its inhabitant. The same burrow may have several external holes connected with it, several inclined channels, which, however, meet at a depth where it becomes vertical. We found constantly the cavity full of water, but this was in March and April; the bottom for several inches was filled with soft and pulpy mud.
>
> There are other instances of burrows somewhat more complex. Their direction may be oblique throughout their whole extent, and composed of a series of chambers or ovoid enlargements, succeed each

other at short intervals sometimes, also, and connected with one of the chambers, a narrow and nearly vertical tubuliform channel extends downward to a much greater depth, and appears to us as a retreat, either during the cold winters or else during the dryness of the summer, when the water is low. That it is not for the mere purpose of escaping pursuit, we infer from the fact that we repeatedly caught the animals in the chambers above, where they remain quietly instead of attempting to disappear into the apartment below.

Tarr (1884) also studied the burrows of *C. d. diogenes* and gave essentially the same description as Girard had given above. Of the chimneys he wrote:

> There is every conceivable shape and size of chimney, ranging from a mere ridge of mud, evidently the first foundation, to those with the breadth of one-half the height. . . . They are always circularly pyramidal in shape, the whole being very smooth, but the outside was formed of irregular nodules of clay, hardened by the sun, and lying just as they fell when dropped from the top of the mound. A small quantity of grass and leaves was mixed throughout the mound but this was evidently accidental.

In many cases the burrows have been found sealed by a plug of mud. Girard (1852) assumed that these plugs were made by the crawfish pulling down the upper layers of the chimney to form a plug for sealing, but most of the workers felt that the plugs were accidental cave-ins. Williams and Leonard (1952) found chela marks under the plug and suggested that the plug was a constructed article. No one knows for certain the method of sealing.

Habitat.—Creaser (1932) found adults in streams, rivers and lakes only during the breeding season in Michigan; he made no mention of the habitat of the juveniles. Hobbs and Marchand (1943) found adults in streams in June and July in the vicinity of Reelfoot Lake, Tennessee, and noted that young specimens (one or two inches in length) are common occupants of streams, and in some of the very small streams they seem to comprise the entire crawfish population.

Penn and Marlow (1959) stated that this crawfish was either a primary or secondary burrower. The adults remain in their burrows except at spawning time; the juveniles burrow along the edges of the bodies of water and in seepage areas, hence they are frequently found in open water. Of the 30 Louisiana lots with ecological data, only 5 are from burrows. The remainder are from aquatic habitats as follows: creeks (52%), ponds and upland sloughs (24%), overflow surface water (16%), and roadside ditches (8%). The majority (72%) were juveniles.

C. d. ludovicianus apparently has a distribution limited by ecological barriers to a relatively small area of Louisiana. It has been found in an area described by Viosca (1933) as the alluvial hardwood ridges and intervening swamps, marshes, and lakes at or near

Gulf level. This area is in southeastern Louisiana around the rim of Lake Pontchartrain and southward to within 50 miles of the Gulf. Only one collection from the Pearl River valley in Washington Parish (*TU*-2964) has been made in a similar habitat above Gulf level. Only four of the fourteen collections with ecological data were made from aquatic habitats, the other ten from burrows (7) and on the surface during heavy rains (3). The burrows excavated do not differ from those described for *C. d. diogenes* by various authors.

As nearly as can be ascertained, *C. d. ludovicianus* is more of a nuisance than a destroyer. The subspecies is plentiful on Audubon Golf Course, New Orleans, and is a hazard only to the golfer's score and temper. It does not destroy vegetation and is found in the lowest sections of the golf course.

Chimneys have been examined up to twelve inches in height and three and one-half inches outside diameter. As many as six openings have been found for a single burrow, some openings being over six feet from the major passage. The water table in this section is less than a foot below the surface, and excavations show that burrows are more than half filled with water. The bottom of the chamber is occupied with soft mud.

Food.—Gastric content examinations have been tried by Penn and associates but with little success. None of the gastric matter was conclusively identified. Laboratory feeding with special diets and examination of the resulting stomach mixture also failed to give comparable food particle analysis. As yet, the exact diet of the crawfish in its natural habitat is in doubt. Better methods will have to be perfected for comparative analysis.

SUMMARY

Color patterns for *Cambarus diogenes diogenes* are twofold: (1) a general dark colored crawfish or olive-green on the dorsal surface, a cream colored ventral surface, red-tipped chelae, and (2) a striped phase with three longitudinal light red abdominal stripes, and essentially the same color pattern as (1) above. Wide variation occurs.

The color pattern for *C. d. ludovicianus* is diagnostic for the subspecies, being brilliant blue with three red longitudinal abdominal stripes, best seen in the juveniles. Adult color is somewhat less brilliant.

Subspecies differentiation between *C. d. diogenes* and *C. d. ludovicianus* is made on the following bases: (1) color patterns; (2) range; (3) cephalic portion of cephalothorax length/areola length ratio of *C. d. diogenes* being 1.44, never ranging below 1.40 and that of *C. d. ludovicianus,* 1.24, never ranging above 1.30; (4) the annulus ventralis of the female *C. d. diogenes* is 1.4 times as wide as long while that of *C. d. ludovicianus* is 1:1; (5) antennal scale length/width of *C. d. diogenes* is less than 1.45, while that of *C. d. ludovicianus* is more than 1.45.

All *C. d. diogenes* in the United States show essentially the same

ratios as given above. This is borne out statistically, except for a small number in Wells Co., Indiana, where the ratio approaches that of *C. d. ludovicianus* but is higher. No explanation is given for this situation.

Ontogenetic variation has been shown to occur for both subspecies, with the cephalic portion of the cephalothorax length/areola length ratio gradually decreasing from juveniles to adults.

Intra-sample specimens, although in large series, have little statistical value in the investigation of subspeciation of *C. d. diogenes,* as shown in large samples from Mississippi.

The range of *C. d. ludovicianus* is limited to the Alluvial Fault Basin in Louisiana. No other specimens have been found in the United States to compare in cephalic portion of the cephalothorax length/areola length ratio and color pattern of this subspecies.

Statistical values based on morphological features are advocated by the author for subspeciation differences within this group of crawfish.

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Notes and Discussion

Color Changes in Oligocottus snyderi Greeley

Oligocottus snyderi is an intertidal fish along the Pacific coast, ranging approximately from central California to British Columbia. During low tides the fish can be found among the algae in pools of water. The fish show considerable variation in color, ranging from a clear translucent green to a dark brown (Bolin, 1944, Stanford Ichthyol. Bull. 3:1). Since field observations often indicated a correlation between the color of the fish and the color of the algae from which the fish were collected, the variation in color may result from the ability of the fish to acclimate to backgrounds of different color.

Two animals were placed in each of a series of plastic dishes of which two were painted black; two, red; and two, white and illuminated by means of 150 ft. c. of light. The fish on the black background were dark brown with little or no evidence of vertical banding. The pigment in both the red and black chromatophores was fully expanded. The fish in the dishes painted red were a lighter brown than the fish in the black dishes and vertical banding was evident, but not pronounced. The pigment in the red chromatophores was fully expanded, whereas the pigment in the black chromatophores was partially contracted. The fish on the white background became pale, with a pronounced vertical banding of alternating light and tan. The vertical bars extended from the dorsal fin to about half the distance to the lateral line. An irregular horizontal bar extended from the base of the pectoral fin to the base of the caudal fin. The pigment in both the red and black chromatophores was fully contracted.

The black chromatophores lay over the white chromatophores. When the pigment in the black chromatophores was contracted, the white pigment contributed to the coloration of the fish, in general, acting to make the fish lighter. The banding was caused by the absence of the white chromatophores in certain areas.

Two animals were placed in each of a series of plastic dishes of which two were lined with brown algae; two, with red algae; and two, with light green algae. The condition of the pigment in the chromatophores was similar

to that described above. The fish on brown algae showed chromatophores with black and red pigment expanded. The black pigment was partially contracted and the red pigment was expanded in the chromatophores of the fish in dishes lined with red algae. On the light green algae, the fish became light, but the banding appeared as described above. The banding that appears in the fish on light backgrounds may function as disruptive coloration; since in the normal habitat of the fish, shadows are cast by the overhanging algae along the sides of the rocks where the fish are found at low tide.

The chromatophores were difficult to stage as the fish were highly excitable and blanched when stimulated. Upon blanching, the fish become a translucent green. All chromatophores were fully contracted. The response occurred in no longer than a minute. The rapidity and nature of the response indicate that the blanching was caused by adrenalin (Odiorne, 1957, *The Physiology of Fishes,* Chapter VIII, Vol. 2). An attempt was made to anesthetize the fish with urethane in order that the chromatophores could be examined more thoroughly. However, this treatment resulted in the fish becoming a little darker, regardless of the background on which the fish were placed.

Because a diurnal rhythm of pigment expansion by day and pigment contraction at night is known for many Crustacea, *O. snyderi* was examined to determine if such a diurnal rhythm existed. Fish were placed in gallon jars that were painted black and covered so that the fish could receive no light. The fish were examined periodically during the day and night for color changes. No rhythm of color change was observed. All of the fish tended to become dark in the dark jars.

The pattern of color changes in *O. snyderi* seems best interpreted as a mechanism that provides protective coloration on the varied backgrounds provided by rock and algae in the intertidal environment.—KENNETH B. ARMITAGE, Department of Zoology, University of Kansas, Lawrence.

Book Reviews

Reproduction in Domestic Animals, Volume I. Edited by H. H. Cole and P. T. Cupps, with a Foreword by Herbert M. Evans. Academic Press, New York. xv + 651 pp., 146 figs., 42 tables. 1959. $14.50.

This book was designed for advanced students and research workers in the field of reproduction, and for clinical veterinarians. The current trend to produce textbooks with multiple authors, each a specialist in his area, has been dictated by economics and by rapid advances taking place in some fields. The multiple-author approach has advantages and disadvantages. Often lacking is a logical development of the subject matter from chapter to chapter. Careful planning has obviated such criticism of the present work. Overriding advantages are the expression of more than one viewpoint, a lessening of the danger of dogmatism, and greater assurance that each chapter will be up-to-date and authoritative.

Seven chapters examine the roles of the endocrines and nervous system in reproduction. Miriam E. Simpson discusses anterior pituitary gonadotropins, the regulation of their production and secretion, and titers and survival times in body fluids. C. W. Emmens considers the gonadal hormones, their effects in embryos, and the results of gonadectomy. Relaxin is discussed briefly. Assay methods are described and there is a short discussion of estrous cycles. Thyroid, adrenal and posterior pituitary hormones are discussed by Charles W. Turner. "Normal" variations in thyroxine secretion rates among individuals of the same species as a result of environmental or genetic influences are emphasized and abnormal states are discussed. Considerable attention is given to thyroid function in birds. The adrenals are treated briefly, as are the effects of oxytocin on smooth musculature, semen transport, and milk let-down. An unusually objective, lucid account of the postulated or established roles of the ovary, pituitary, placenta, and fetal hormones in pregnancy, and of the less direct effects of certain other endocrine substances, is presented by Hubert R. Catchpole. Generalizations are followed by a short but informative consideration of some special aspects in domestic species. Hormonal factors affecting gestation length and the onset of parturition are described by M. T. Clegg. A table of the gestation periods of fifty-eight common breeds of livestock is included. Joseph Meites considers hormonal requirements for mammary growth and lactation, and reviews theories relating to the inhibitions of lactation during gestation and its onset at parturition. A discussion of milk yields after hormone treatment will interest dairy scientists. An excellent discussion of present knowledge of neural factors affecting the release of pituitary gonadotropins, mating behavior, parturition and lactation is presented by William F. Ganong. Considerable attention is given to the experiments relating to the role of light in stimulating reproductive processes in birds and ferrets.

Five chapters describe the estrous cycles of the cow (William Hansel), mare (Victor Berliner), ewe and dow (T. J. Robinson), sow (J. M. Boda), and dog (A. C. Andersen and Eloise Wooten). Cyclic changes in the reproductive organs, endocrines, and in behavioral patterns are delineated and techniques of external control of the cycles are presented. The collection of these data into one volume has been a valuable service to students of mammalian reproduction.

Four chapters are concerned with the anatomy of reproductive organs of certain domestic forms, extraembryonic membranes and placentas of artio-

dactyls, perissodactyls, and carnivores, and conventional descriptions of meiosis, maturation, ovulation, gamete transport, fertilization and cleavage. Contributors are Lemen J. Wells (female organs), Logan M. Julian and Walter S. Tyler (male organs), C. R. Austin (fertilization and early embryology), and Elmer B. Harvey (extraembryonic membranes). That the editors felt obliged to include these chapters in an advanced work suggests they may have misgivings concerning the academic preparation of some segments of their audience for advanced study and research. These chapters are well-written and in no way detract from the excellence of the book; but, they do add to consumer costs. Comparative anatomists will find interesting reading in several of these chapters.

Each chapter cites a wealth of pertinent literature. There are 1,324 references in the seven chapters on reproduction physiology alone. Many excellent original tables, graphs, drawings, and photomicrographs supplement the text throughout. There is an Author Index of 31 pages as well as a usable Subject Index. Together with parts of Gorbman's *Comparative Endocrinology,* Velardo's *Endocrinology of Reproduction,* and Pincus and Thimann's *The Hormones* (the last also by the Academic Press), much of the present work should be required reading for every serious student of reproduction physiology.—GEORGE C. KENT, JR., Louisiana State University, Baton Rouge.

A FLORA OF SOUTHERN ILLINOIS. By Robert H. Mohlenbrock and John W. Voigt. Southern Illinois University Press, Carbondale. ix + 390 pp., 10 pls., 67 figs. 1959. $7.50.

This attractively styled manual will be of interest to botanists in several Midwestern states, since the flora of southern Illinois includes a considerable number of different floristic elements which grow in a rather wide range of habitats. The handsome printing and well-selected photographs should add considerably to the appeal of the book for students.

The ecological approach of the authors should also make the book stimulating for class use, since it emphasizes the behavior of species as components of living vegetation rather than as morphological types. On the whole the keys appear to be well-constructed and easy to use, although the lack of any additional descriptions for individual species may make it easy for students to go astray in such complicated genera as *Desmodium.*

It would be unfair to criticize adversely such a carefully prepared work as this, but the reviewer would like to make a few suggestions which might be considered in future editions. The author's alignment of taxa in the sequence as they are keyed out but without any numbers (except for families) can lead to confusion. This is especially true in large families such as the Leguminosae and Compositae, where the user of the key to genera may have to thumb through a number of pages looking for the genus. It would seem preferable to either arrange genera alphabetically within the family, or better, to number them.

A striking omission in the book is the lack of a map showing the area covered by the flora and the more important localities. For those using it as a field manual or interested in local plant distribution, such a map would surely be a great convenience. A short glossary of botanical terms would also be useful but is not absolutely necessary since students presumably would have access to other textbooks.

These are all minor points, however, and it should be emphasized that the *Flora* appears to be quite adequate for use in its present condition. The authors have certainly succeeded in their goal of publishing a book which will interest

amateur naturalists as well as applied biologists. It is to be hoped that other regions in the Midwest may someday be supplied with floristic treatments as well done as this one.—GRADY L. WEBSTER, Purdue University, Lafayette, Indiana.

GUIDE TO THE REPTILES, AMPHIBIANS AND FRESH-WATER FISHES OF FLORIDA. By Archie Carr and Coleman J. Goin. University of Florida Press, Gainesville. Reissue, 1959. 341 pp., 30 figs., 67 plates. Cloth $8.00.

The first printing (1955) of this attractive guide to the cold-blooded vertebrates of Florida was so well received as to warrant a reissue. The continued demand is a tribute to the lucid descriptions, informative illustrations, and well-constructed keys. The use of the latter by the uninitiated is enhanced by excellent text figures depicting basic morphology and by inclusion of an adequate glossary for each group treated.

While this is a reissue and not a revision, the reversed legend of Plate 10, present in the 1955 issue, has been corrected.—ROBERT E. GORDON, University of Notre Dame, Notre Dame, Indiana.

MANUAL OF VEGETATION ANALYSIS. By Stanley A. Cain and G. M. de Oliveira Castro. Harper and Brothers, New York. 325 pp. Illus. 1959. $7.50.

It has been frequently asserted that the usual phytosociological methods and concepts developed in the temperate regions are inapplicable to the tropics. One of the virtues of the present manual is that it devotes part of its space to a consideration of phytosociological techniques as applied to tropical forests in Brazil. Although not a study of tropical vegetation per se, "it does recognize the existence of the tropics and some of its problems, and that is something." Since the tropics are notably underrepresented in ecological literature, this emphasis is timely and might have been used as the basis of a subtitle for this volume.

The authors have envisioned the manual as providing a guide, not a "cook book" of recipes, to vegetational analyses at all levels — from preliminary reconnaissance with a large descriptive and subjective, even intuitive, component to more restricted and thus more intensive and objective studies. The aims, research facilities and time available will, as the authors point out, condition the selection of the concepts and methods used. Concepts and methods of both European and American schools of phytosociology are included.

An early chapter on floristics acknowledges the debt and relationship of phytosociology to plant geography. This reviewer, whose work has largely been in phytosociology, was surprised recently to find that he was regarded by some ecologists as a plant geographer; ecology properly being reserved for physiological ecology or autecology. The view of the authors that studies of vegetation are a "logical antecedent to physiological-ecological work" makes the reviewer again a "comfortable ecologist."

The discussion of reconnaissance points out the danger of being misled by seeing only the flood plain forests along the main arteries of transportation, the rivers, much as the early explorers of eastern North America saw what seemed a continuous pine forest. Some danger exists in more developed regions that ecologists may see largely what borders on the highways.

A substantial portion of the manual is devoted to a discussion of the tra-

ditional quantitative analytic and synthetic characteristics of plant ecology with briefer coverage of the qualitative characteristics. Most of this material is not new, although contemporary textbook coverages are not as up to date nor as clearly and comprehensively stated. Of particular interest is the exemplification of these characteristics in a tropical vegetation, the rain forest, although the book is not restrictive in its application. The authors warn against becoming circumscribed by method and make clear that there is no universal approach to vegetational study or description.

The discussion of the techniques and problems of sampling and the phytosociological measures, frequency, density and dominance is clear and comprehensive as might be expected, since the senior author has made major contributions in this area of ecology. This reviewer believes that more attention might have been given to the more recently developed rapid sampling methods particularly emphasizing their relative speed and efficiency. Raunkaier's "Law of Frequency" is critically considered and misunderstandings surrounding it are clarified. The concept and utility of minimal area is examined at length. However, the use of the minimal area to determine the size of quadrat as cited in the manual has been questioned, most recently by Grieg-Smith in his "Quantitative Plant Ecology."

Methods of combining the characteristic measures of number, coverage and pattern for purposes of description and analysis of communities are described and various useful tabular and graphic methods outlined. The use of the term "combined frequency" for the average frequency of a species in several stands may lead to some confusion especially, since the glossary describes it as the "total figure" which implies the sum of the several frequencies.

The last chapter deals with the use of life form and leaf size as a means of describing and classifying vegetation.

In brief, the manual provides a spectrum of phytosociological methodology, well presented and affording an excellent introduction to the specialized and extensive literature on the subject of vegetation study. The reader is not led in the path of phytosociological righteousness but is provided with various caveats and urged to select the methods appropriate to his own aims and needs. —ROBERT P. MCINTOSH, University of Notre Dame, Notre Dame, Indiana.

RADIATION, GENES, AND MAN. By Bruce Wallace and Th. Dobzhansky. Henry Holt and Company, Inc. 205 pp. 1959. $3.50.

This timely book gives a scholarly presentation of one of the more urgent scientific problems today, namely, an evaluation of the magnitude of genetic radiation damage to human populations. The argument of the authors can be reduced to the following points: Radiation induces gene mutations. The vast majority of mutations are harmful. Mutations introduced into the human population may harm individuals for many generations to come. Consequently, radiation exposure must be kept to an unavoidable minimum. The problem of determining what constitutes an unavoidable minimum is extremely difficult, since, in our present society, it is impossible to eliminate radiation exposure, and, indeed, increasingly difficult to keep radiation exposure from encompassing larger and larger segments of the population. The authors point out that the most important source of radiation to which human populations are at present exposed is neither background radiation, nor atomic bombs, but the X-ray machines in hospitals and in doctors' offices. Of increasing importance is the fact that more and more persons are employed by industrial plants that use X

or gamma radiation to inspect their products. The use of nuclear energy for the production of power on a large scale is imminent.

The authors present in lucid style a thorough treatment of the basic scientific facts of radiation physics, genetics, and, particularly, population genetics, all of which are necessary information for anyone who wishes to pass judgment on whether — or, rather, to what extent — man should be exposed to radiation.

The authors show an admirable open-mindedness in presenting both sides of the controversy, and make it very clear that there are broad areas in which our present scientific information is woefully inadequate. The need of experimentation with mammals to test the validity of extrapolating information secured with lower forms of life is an acute need. The difficulty or impossibility of experimenting with humans is a serious limitation.

Of particular interest is the authors' treatment of radiation damage and value judgments. We must decide, for example, whether in the detection and treatment of various diseases the genetic damage we are inflicting on succeeding generations by the inadvertent, and, for practical purposes, unavoidable exposure of human germ cells to X-rays plus the chance of inducing leukemia or other malignancy in the person examined outweigh the benefit of early detection and possible cure of the disease under consideration. In reaching such decisions, the benefits expected from a given course of action must be weighed against the risks incurred. Decisions of this kind, the authors point out, will depend to a large extent on the ethical standards or basic philosophy of a given person, group, or commonwealth. We cannot disregard the damage that will befall future generations, even though our emotional involvement in these generations is slight.

This book should be required reading and *study* for anyone before he makes any pronouncement concerning the effects of radiation on the human race. —C. S. BACHOFER, C.S.C., Department of Biology, University of Notre Dame, Notre Dame, Indiana.

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Studies on the Collembolan Genus Hypogastrura

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In earlier papers I have indicated the importance of chaetotaxy in the taxonomy of Collembola. Recently I have become particularly interested in the genus *Hypogastrura,* one of the most archaic genera of the order. The genus as so far known includes about a hundred cosmopolitan species. The species treated in this paper are not numerous and the specimens available for study few in number, yet it is quite possible that the general trends in the chaetotaxy of the group can be seen here, and the conclusions drawn from this material are probably applicable to most of the members of the genus.

A number of my colleagues of collembology furnished much of the material upon which this study was made. I wish to extend my sincere thanks to Dr. K. Christiansen (USA), Dr. D. L. Wray (USA), Dr. Marie Hammer (Denmark), and Dr. F. Carpentier (Belgium). The specimens described in this paper are in my personal collection. The study of the chaetotaxy of this group has already been outlined by Bonet (1945, 1947), Stach (1946), Gisin (1946, 1949), and Yosii (1956). In the last mentioned paper I described the basic chaetotaxy in the Family Hypogastruridae and named each seta of the head and body segments. This nomenclature is followed in the present paper, although it should be noted that the form that I originally described as typical of *Hypogastrura* is actually that found in a member of *Ceratophysella,* and thus some modifications must be made. For convenience, the setae are illustrated in the Key Figure together with abbreviations of technical terms used in the description of species.

The 20 species of *Hypogastrura* here treated and described, and those whose chaetotaxy is already known, may be split into three subgenera as follows:

1. S.s. upon Th. II, III is p_4 2
   S.s. upon Th. II, III is p_3 Ant. III/IV with or without eversible antennal sac .... *Ceratophysella*
2. Accessory tubercle of P.A.O. is enclosed by two posterior tubercles of that organ. Eversible antennal sac usually present .... *Cyclograna*
   Accessory tubercle of P.A.O. is located apart from it. Eversible antennal sac absent .... *Hypogastrura*

Subgenus *Ceratophysella* Börner, 1932
Type: *Hypogastrura* (*C.*) *armata* Nicolet

The subgenus may be divided into groups in the following manner:

1. Upon Abd. IV, p_1 longer than p_2. M_1 upon Abd. I-III absent 2
   Upon Abd. IV, p_1 shorter than p_2. Small m_1 upon Abd. I-III present .... *communis* Group
2. Upon Abd. IV both p_2 and p_3 short. S.s. is p_5 ....*armata* Group
   Upon Abd. IV, p_2 short and p_3 long. S.s. is p_4 ....*denisana* Group

THE COMMUNIS GROUP

This group has the chaetotaxy of Gisin's a-Type (1947) and is represented by the figure of *H. troglodites* Yosii and *H. communis exilis* Yosii 1956.

Hypogastrura communis (*Folsom*)
Fig. 2

Folsom, 1897, Kinoshita, 1916; Denis, 1927, 1936.

Syn. nov. *Hypogastrura yuasai:* Yosii, 1954 Oyo-Kontyu **10**:137.

The species has been thoroughly studied by Denis 1924, 1925 with Japanese and Indian material. The species is clearly different from *H. armata* in the chaetotaxy of Abd. IV, where p_2 is greater than p_1 and p_3. This type of chaetotaxy is represented in Europe by *H. denticulata* Bagnall 1941 (*see* Gisin 1949). The species has some color variations.

Hypogastrura communis f. **principalis** (nov. forma)

Body color intensely blue black. This type is very common in central Japan and frequently emerges in huge numbers from decaying straw in rice fields in late autumn. It is also found in China and Kashmir. *H. yuassai* Yosii, 1954 from Japan is a synonym of the present form. Recently I examined some individuals of this species from Okinawa (M. Nagayama, collector).

H. communis f. *exilis* Yosii

Syn. *H. communis exilis,* Yosii 1956.

Body color brownish gray or dark brown. This color form is abundant in Japan all through the year and is often fungivorous or cavernicolous. What I have previously reported from Taiwan as *H. armata* Nic. is, in reality, the present form.

Specimens seen.—I have seen 10 specimens from North America (all from Banff, Alberta, Canada) referable to the present species (31 VII 1950, K. Christiansen). Another 20 specimens from Back Bone Mt., vicinity of Thomas, West Virginia (18 VI 1950, K. Christiansen) are also referable to the present form. The latter are rather young individuals and not to be determined with certainty.

The following species are to be included to the *communis Group*:

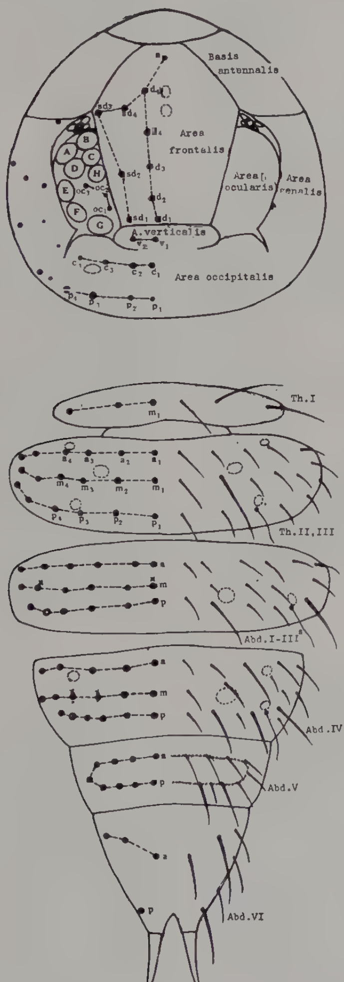
H. troglodites Yosii, 1956.—Antenna without eversible sac. Body color pale; Japanese caves.

H. quinqueoculata Yosii, 1956.—Eyes 5 per side. Dentes with 5 setae; Japanese caves.

H. fukugakuchiana Yosii, 1956.—Eyes 4 (or 3) per side. Dentes with 6 setae; Japanese caves.

H. proserpinae Yosii, 1956.—Eversible antennal sac rudimentary. Dentes with 6 setae. Mucro without outer lobe. Abd. IV with s.s. at the position of P_4. (Fig. 3.)

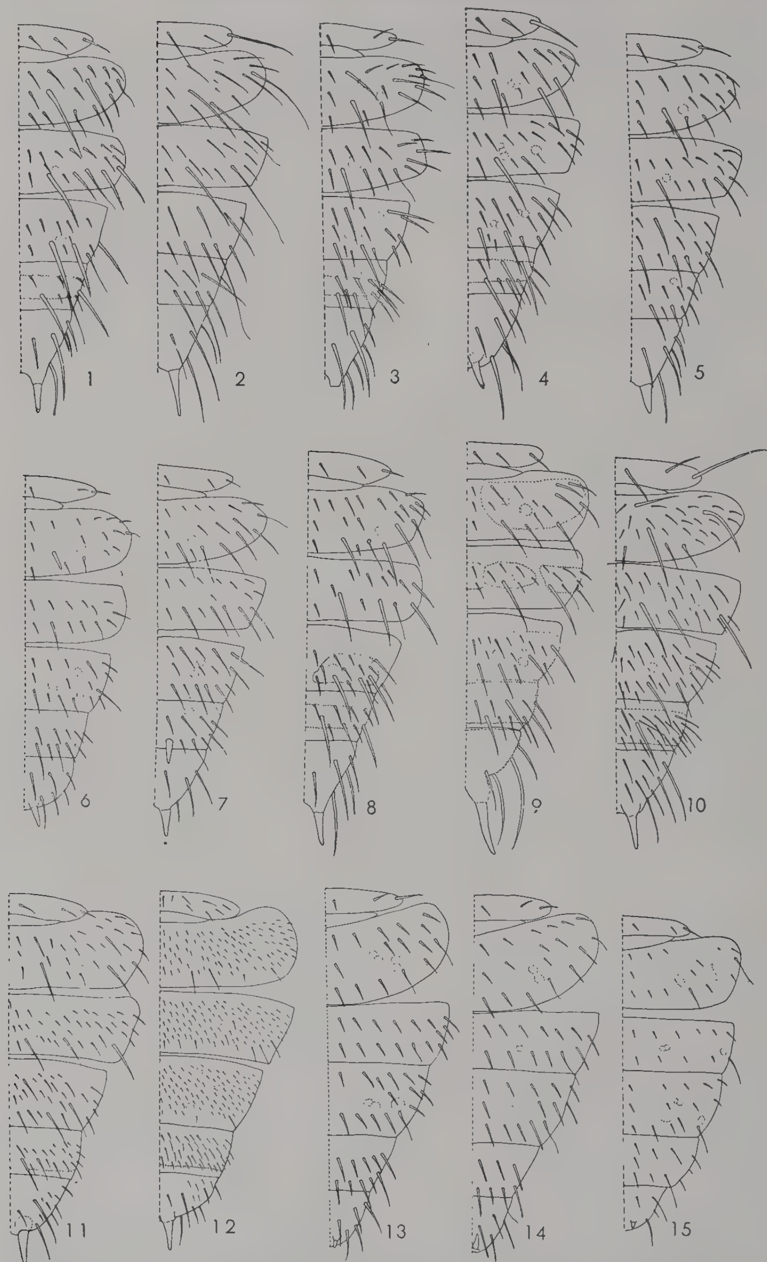
H. denticulata Bagnall, 1941.—Unguis very slender; England, Switzerland.



Key figure.—Illustration of a typical hypogastruran with abbreviations for the nomenclature of each seta. The right side of the head shows its subdivision into areas; the left, the distribution and nomenclature of the setae. The lower portion of the illustration shows the tergites and setae of *Ceratophysella communis* (Folsom). (Setae with an "x" are missing in the example.)

Abbreviations for the nomenclature of each setae. HEAD: a — unpaired anterior seta on Area Frontalis; d_{1-5}—dorsal setae of Area Frontalis; sd_{1-5}—subdorsal setae of Area Frontalis; oc_{1-3}—ocular setae of Area Frontalis; (suffix number indicates each seta counted from the proximal one as 1, 2, 3——); v_{1-2}—vertical setae of Area Verticalis; p_{1-4}—parietal setae of Area Occipitalis; c_{1-4}—cervical setae of Area Occipitalis; (suffix number indicates each seta counted from the dorsal one as 1, 2, 3——). TRUNK: s.s.—seta sensualis, a specially modified seta of the tergite, usually more slender than others and with broad socket; a-row—anterior row of setae on each tergite; m-row—middle row of setae on each tergite; p-row—posterior row of setae on each tergite; (a_{1-6}, m_{1-6}, p_{1-6} indicates each seta counted from the dorsal one as 1, 2, 3——).

Other abbreviations: Ant. I-IV—the 1st, 2nd-4th antennal segment; Th. I-III—fore, middle and hind thoracal segment; Abd. I-VI—the 1st, 2nd-6th abdominal segment; Ung_{1-3}—Unguis of the fore, middle and hind legs; P.A.O. — postantennal organ; fovea—rounded spot of the integument, where the skin granules are wanting; fovula—rounded spot of the integument, where the skin granules are minute; AH—anal horns; Man—manubrium; D—dentes and Mu—mucro.



Figs. 1-15.—1. *Hypogastrura* (*Ceratophysella*) *communis* (Folsom). 2. *H.* (*Ceratophysella*) *proserpinae* Yosii. 3. *H.* (*Ceratophysella*) *armata* Nicolet. 4. *H.* (*Ceratophysella*) *pseudarmata* (Folsom). 5. *H.* (*Ceratophysella*) *deni-*

Questionable species of the *communis Group*:

H. engadinensis Gisin, 1949.—Eversible antennal sac rudimentary or absent; Switzerland.

H. succinea Gisin, 1949.—Dentes with 6 setae. Anal spines succinic in color; Switzerland, Germany, Jan Meyen Is.

THE ARMATA GROUP

The chaetotaxy of this group represents Gisin's b-type (1947). I have seen only two species belonging to the group, although they seem to be common in Europe.

Hypogastrura armata (Nicolet)
Fig. 3

Nicolet, 1841; Börner, 1932; Stach, 1949; Gisin, 1949.

The diagnostic structures of this species have already been described by Stach and other authors. Chaetotaxy of head normal. Ventral side of antennal segment IV has 10-15 small, peg-like setae. Th. II, III with setae in three rows (a-, m-, and p-). S.s. is at the position of p_3 and is as large as p_2. M_2 is rather long and often dislocated somewhat distally. Small pit before s.s. One additional s.s. lateral at the position of m_6. Abd. I-III with setae in two rows (a- and p-). P_5 is s.s.; p_2 is longer than the other setae of the row. No m-row dorsally. Abd. IV with setae in three rows. P_1 is much larger than subsequent p_2 and p_3. P_4 is again large. P_5 is s.s. and as long as p_4 but slender. Abd. V with coarsely granulated area at about its middle. Setae in two rows, arising from the margin of this area. P_1 larger than p_2. P_3 appears to be a little modified. Abd. VI with s.s. as usual.

Specimens seen.—One example from Grunwald, München, Germany (R. Yosii, collector). This supposedly well-known species is known with certainty only from Europe. All records from other parts of the world must be tentative until their chaetotaxy is examined.

Hypogastrura pseudarmata (Folsom)
Figs. 4, 24-29

Syn. *Achorutes pseudarmata* Folsom, 1916.

Length 1.5 mm. Color dark brown or blackish brown. Ant. IV has an end-bulb slightly divided into two parts, accompanied by a socket hair and some weak setae. There are also slender and well-defined sensory setae, seven dorsally and about twenty small, peg-like setae ventrally. As all specimens were rather contracted, the eversible antennal sac was not seen, but it may be present. The organ of Ant. III normal and with two accessory setae. P.A.O. in deep fold of the integument. Two anterior elements are much larger than the posterior ones. An accessory tubercle is very conspicuous. All of these organs

sana Yosii. 5. *H.* (*Ceratophysella*) *glancei* Hammer. 7. *H.* (*Ceratophysella*) *duplicispinosa* Yosii. 8. *H.* (*Cyclograna*) *vulgaris* n. sp. 9. *H.* (*Cyclograna*) *loricata* n. sp. 10. *H.* (*Cyclograna*) *horrida* n. sp. 11. *H.* (*Cyclograna*) *gibbomucronata* Hammer. 12. *H.* (*Cyclograna*) *pilosa* Yosii. 13. *H.* (*s. str.*) *nivicola* (Fitch). 14. *H.* (*s. str.*) *copiosa* (Folsom). 15. *H.* (*s. str.*) *christianseni* n. sp.

together are about as large as one eye in diameter. Tibiotarsus has one tenent hair, whose distal end is slightly knobbed, or blunt. Unguis elongate, distally acuminate and with one inner tooth and a pair of lateral teeth. Unguiculus setaceous, about two-thirds as long as the unguis and with a broad basal lamella. Ventral tube with four setae per side. The rami of the tenaculum with four teeth. Dentes of the furca coarsely granulated on dorsal side and with seven setae almost of equal length. Mucro granulated along its shaft and is typically of *armata* type. Anal spine smaller than that of *H. armata* and is about two-thirds as long as the mucro of the third unguis (inner side). Anal lobe well developed. The profile of Abd. VI quite different from that of *H. armata* (Folsom, 1917). Chaetotaxy typical of the type; but s.s. is so poorly developed upon Th. II, III, and Abd. I, as to be found only by the neighboring pit, which is very conspicuous. Abd. I-III with two rows of setae. P_5 is s.s., small on Abd. I and normally long on Abd II and III. M_1 is absent. Abd IV with three rows of setae. P_1 is large while p_2 and p_3 are small. Abd. V with a granulated middle area.

Specimens seen.—Fifteen specimens from Arlington, Massachusetts, USA. (15 XI 1950, K. Christiansen.)

I have two specimens of *H. sigillata* Uzel to which the species is closely allied. These specimens were collected in arctic Canada and sent by Dr. Marie Hammer. The specimens were already mounted and I could not observe all the setae of the body. Yet s.s. of Th. II is well developed. These two species must therefore be separated.

The following species are to be included in the *armata* group:

H. gibbosa Bagnall, 1940; Gisin, 1949.—A pair of setae of Area Ocularis and of Area Frontalis converted to spines; England, Switzerland.

H. granulata Stach, 1949.—Abdominal segments with granulated areas; Poland, Ukraine, Slovakia.

H. luteospina Stach, 1919.—Anal horns queerly modified; Poland, Ukraine.

H. cavicola Börner, 1901; Stach, 1949.—Eversible antennal sac absent, body color reduced; caves of Hungary, Austria, and Germany.

Typhlogastrura balazuci Delamare, 1951.—From a French cave; has chaetotaxy of the *armata* type.

THE DENISANA GROUP

This is apparently a branch of the *armata Group*. On Abd. II-III, m_1 is always absent as in *H. armata*. An Abd. IV, however, p_1 is large, p_2 small, and p_3 is absent. So, s.s. is the position of p_4, instead of p_5 as in the *armata*-type. Generally, m_2 on Th. II, III has a tendency to move posterior near to p_2.

Hypogastrura denisana Yosii

Fig. 5

Yosii, 1954, 1956.

As figured in Yosii, 1956 (Plate IV, Fig. 38), m_2 on Th. II, III and p_2 on Abd. I-III are large. Abd. IV has the chaetotaxy as stated above. I have erroneously described the s.s. of this segment as p_5

(*loc. cit.*, p. 17). It is actually p_4. On Abd. V, the setae of p-row are larger than a-row (erroneously figured in Fig. 38). The species is distributed all over Japan.

Hypogastrura glancei Hammer
Fig. 6

Hammer, 1953.

Type specimens sent to me by Mrs. Hammer reveal the chaetotaxy of *denisana*-type. Body setae relatively small. Th. II, III with m_2 thicker than others, but not especially long and often moved near to P_2. P_3 is s.s. and not long. Abd. I-III with p_2 larger than others, and p_5 s.s. Abd. IV with p_1 largest, p_3 second largest, and p_2 small.

Specimens seen.—Two specimens from Coppermine, Arctic Canada (M. Hammer, collector).

Hypogastrura duplicispinosa Yosii
Fig. 7

Yosii, 1954, 1956.

As has been stated, the species has the *denisana*-type of chaetotaxy. P_1 on Abd. V is converted to a spine; Japan.

I can find no reliable data to place other species in the *denisana* Group. Only *Schafferia duodecimocellata* Bonet, 1946 from a Mexican cave has the chaetotaxy of *denisana*-type.

Subgenus *Cyclograna*

The subgenus includes species characterized by the peculiar forms of the P.A.O. In the chaetotaxy, s.s. on Th. II, and III is p_4 in contrast to p_3 in the subgenus Ceratophysella. The eversible sac of the antenna is always present among known forms of *Cyclograna*. Some species of the group have setae of the head converted to spines (*H. franzi, pilosa, horrida,* etc.). The subgenus has the tendency towards increased body setae. The first step is seen in *H. horrida* and *H. gibbomucronata* in which, although the arrangement of setae is irregular, one may find larger setae distinctly different from others in each position. Such a condition, I should like to designate as "Plurichaetosis." This augmentation of setae continues until there is no longer any distinction between individual setae, and the body segments are covered uniformly with many small setae (*H. pilosa*). To such a state of chaetotaxy, I have proposed the name "Polychaetosis."[1] Such polychaetosis is not only found in *Cyclograna* but also in such genera of the arthropleon collembola as *Anurida, Homaloproctus,* and *Tetrodontophora.* Examples of plurichaetosis include almost all species of the genus *Onychiurus,* which has arisen apparently from *Tullbergia* in which the chaetotaxy is not at all complicated.

Hypogastrura (Cyclograna) vulgaris n. sp.
Figs. 8, 30-36

H. armata: Folsom, 1916.

Length 1.3 mm. Color bluish-gray. The pigment is aggregated

[1] R. Yosii, in 80th Jubilee Volume of Prof. Stach of Krakow (in Press).

into patches. Antennae dark. Legs, furca, and ventral side of the body pale. End-bulb of Ant. IV located in a groove and accompanied by many setae with basal sockets. There are seven elongated sensory hairs dorsally and about twenty-five small, but very conspicuous, peg-like setae ventrally. Ant. III/IV with eversible sac. Third antennal organ is of two small rods in a shallow groove accompanied by two slightly modified setae. Eyes eight per side upon black eye-patches. P.A.O. is Gisin's h-type, i.e., the anterior two elements are situated almost in a straight line, while the posterior two have between them an elliptical accessory tubercle. Unguis elongate and with one internal tooth and a pair of lateral teeth. Unguiculus setaceous, reaching to about one-half of the unguis and with a rounded basal lamella. Tenent hair is not especially differentiated and not swollen at apex. Ventral tube with three (?) setae on each side. Rami of the tenaculum with four teeth. Mucro typically of *armata*-type, with broad outer lobe and basally granulated. Dentes dorsally granulated and provided with seven setae of which four on the inner side are remarkably thickened. Dentes to mucro as 2/1. Mu/Ung_3 as 2/3. Anal spines well-developed, very long with basal papillae touching at their bases. Anal spine (papillae included) to Ung_3 as 17/9. Chaetotaxy of head normal. Base of antennae well separated from frontal area by smaller granulation of the integument. The setae of the latter normal, d_2 stronger than others and positioned more lateral than usual. Segmental margins of the trunk with finer granulations than the middle portion and their boundaries of the finely granulated areas well defined. Th. I with 3 + 3 setae in a row. Th. II, III with three rows of setae. P_2 is long. M_2 is short. S.s. is p_4. Abd. I-III with two rows and with a small m_1 as in *H. communis*. A_2 lies more lateral in position than usual. Abd. IV is distinctly tuberculated laterally and all setae except a_1 are located here. The arrangement of these setae is of the *communis*-type. Abd. V with two rows of setae. The segment is coarsely granulated at the middle portion. P_1 is extremely large and often dislocated anteriorly.

Holotype.—One male from Corvallis, Oregon, USA. (21 XII 1949, V. Roth, collector).

Paratypes.—Twelve specimens from the same locality and ten from Cambridge, Massachusetts, USA (25 IX 1949, K. Christiansen, collector).

Judging from Folsom's figures (1916, Proc. U.S. Nat. Mus. 50: 491) this species may be the same as his *H. armata*. Whether the present name becomes synonymous with Packard's *A. boletivorus, texensis, marmoratus* or *pratorum* must be determined after examining his type specimens.

Hypogastrura (Cyclograna) loricata n. sp.
Figs. 9, 37-40

Body length 1.7 mm. Color dark brown or brownish gray. Antennae well-pigmented. Segmental margins, ventral side of body, and

extremities paler. Ant./Head as 7:10. Ant. IV with an end-bulb deeply inserted in a groove accompanied by some socketed setae. Dorsally, there are seven sensory hairs of relatively small size. Peg-like setae of the ventral side are small but numerous. Ant. III/IV with an eversible sac. Only two accessory hairs of the third antennal sense organ can be seen. A sensory groove with two rods is apparently present, each masked by the rough granulation of the skin. Ant. II and I each with only one row of setae. Each antennal segment is very coarsely granulated and sharply contrasted with their minutely granulated borders. The antennal bases and the cervical margin are minutely granulated, in contrast with the frontal area. Eyes eight on a side, upon black patches. P.A.O. of *vulgaris*-type. Setae of frontal area very long and $3 + 3$ in number; sd_1, sd_4 and sd_5 are converted into spines. Area verticalis separated from other parts by a furrow and v_2 is much longer than v_1. Unguis normal with one internal tooth and one lateral tooth. Unguiculus setaceous, with two rounded, broad lamellae. Tenent hair absent. Ventral tube with $4 + 4$ setae. Rami of the tenaculum with four tenent. Dentes of the furca dorsally granulated with seven setae; the three setae of the inner row are thick. Mucro distally rounded with a broad, hyaline outer lobe. Each segment of the body with a remarkable granulated portion at about the middle zone. Upon Th. II, III and Abd. I-III, these granulated portions are divided medially by finely granulated areas along the dorsal midline and where a_1, m_1, and p_1 or a_1 and p_1 are located. Other setae are all on the granulated area. Upon Th. II and III, p_2 and p_5 are long. S.s. is p_4, which is small and often dislocated proximally. On Abd. I-III the coarsely granulated area is relatively small. M_1 is distinctly present. P_2 and p_4 are long. S.s. is long and in position of p_5. Abd. IV with three rows of setae. The segment is coarsely granulated on the anterior two-thirds of the segment, and it is not divided medially. P_1 and p_2 almost equally long. P_3 is small. P_4 is s.s. (?). Abd. V coarsely granulated over most of the segment except its margin. This condition is in contrast to the granulation of Abd. V in other species such as *armata, communis,* and *vulgaris,* where only the portion between two rows of setae is coarsely granulated.

On Abd. VI, the granulations are extremely coarse upon the papillae. These, in turn, are so large that the segment is constricted on their bases, where a_1 is inserted. Anal horns (AH) very long, yellow in color and gradually tapering to the end. AH/Mu as 2:1. AH/$Ung._3$ as 4:3.

Holotype.—One male from Mount Washington, New Hampshire, USA (30 VIII 1949, K. Christiansen, collector).

Paratype.—Eight specimens from the same lot.

The species exhibit no plurichaetosis and may be distinguished from other species by three cephalic horns per side and the peculiar granulation of the integument.

Hypogastrura (Cyclograna) horrida n. sp.
Figs. 10, 41-45

Body length 1.6 mm. Color chestnut brown. Dorsal side of the body mottled with dark spots. Ant/Head as 17:15. Ant. IV with an end bulb concealed in a groove, accompanied by a conspicuous socket-seta. Sensory hairs of dorsal side more than 5, slender and well-developed. Ventral side thickly beset with numerous peg-like setae, more than fifty in number. Ant. III/IV with eversible sac. Third antennal organ and companion setae normal. Area Antennalis of the head clearly distinguishable from Area Frontalis which carries elongated, filiform setae and two cephalic spines per side which represent sd_4 and d_5. P.A.O. typical for *Cyclograna*. Eyes eight per side, upon black patches. Area Verticalis is distinctly separated. Th. I with 3 + 3 setae in a row. All segments beyond Th. II are very unusual in their chaetotaxy. Although the distinction between large and small setae is still preserved, the small setae are numerous and irregular in position (plurichaetosis). On Th. II, III, one may find along its posterior margin p_2, p_4 (s.s.), and large a_2 and m_5 (?). On Abd. I-III, p_2, p_4 and p_5 (s.s.) are large. Upon the segments beyond Abd. IV, s.s. is no longer seen. The integument is regularly granulated and each segmental margin has finer granulation. The larger granules increase in size posteriorly on Abd. IV-VI, and Abd. V is distinguished by two coarsely granulated zones at about the middle of the segment. Anal horns elongate, yellowish brown in color, and located upon conspicuous papillae which are somewhat separate. The longest setae of the body are not feathered. Unguis normal. Unguiculus setaceous, half as long as the unguis, and with rounded basal lamella. Tenent hairs not apparent. Ventral tube with four setae per side. Dentes of furca dorsally granulated and with seven setae (5 thick and 2 normal). Mucro with well-developed outer lobe and rounded apex.

Holotype.—One female from Corvallis, Oregon, USA (26 XII 1950, V. Roth, collector).

I have seen some individuals from the Japanese alpine region which are very near to the present form. As they are apparently immature, I am awaiting new material before determining them.

Hypogastrura (*Cyclograna*) *gibbomucronata* Hammer
Fig. 11

Hammer, 1953.

A type-specimen sent by Hammer is plurichaetotic. Setae upon head normal in position. Area Frontalis somewhat coarsely granulated. D_2 and sd_4 larger than others. Th. I: 3 + 3 setae. Th. II, III: setae of the posterior row fairly normal in position. P_4 is s.s. and not large. The other rows are plurichaetotic except along the median dorsal line. The plurichaetosis is more prominent upon Th. III than on Th. II. Abd. I-III with p-row showing a clear distinction between large and small setae. S.s. is situated just posterior to a fovea. Abd. IV with p-row normal in location. P_5 is s.s. Abd. V with a coarsely granulated area at about the middle of the segment. Setae approxi-

mately in two rows and p_3 is s.s. Abd. VI is polychaetotic laterally. A_1 is relatively small and is placed just before the anal papillae. A_2 is large.

Specimens seen.—One specimen from Reindeer Station, Arctic Canada (M. Hammer, collector).

Hypogastrura (Cyclograna) pilosa Yosii
Fig. 12

Yosii, 1956.

The chaetotaxy of this interesting species showing typical polychaetosis has already been described. In the present report, I will add only the figure showing all body segments. The species is known only from middle and southern Japan.

As the subgenus *Cyclograna* is characterized by its peculiar P.A.O., the species belonging to it are easily recognized from the literature. They are:

H. franzi Butschek et Gisin, 1949.—D_2 and sd_4 of the frontal area converted to spines; Austria.
H. hystrix Handschin, 1924, Gisin, 1949.—Dens with 5 setae, body hairs strongly barbulate; Switzerland, Austria.
H. californica Bacon, 1914.—One long spine on each segment; USA.

We have in addition to these two species with multituberculate P.A.O. and mucro similar to that of *H. armata.*
Mitchellania hermosa Wray, 1953.—Head with two spines per side; USA.
H. monstruosa Gisin, 1949.—Setae of Abd. IV of *communis*-type; Switzerland.

Subgenus *Hypogastrura* Bourlet, 1939 (*sensu* Gisin, 1955)
Type: *Hypogastrura (H.) viatica* (Tullberg)

The subgenus is characterized by the position of s.s. on Th. II and III, and by the lack of an eversible sac on the antenna; as well as by the relatively small and simple form of the P.A.O. Body setae usually short and the difference between long and short setae not conspicuous. We may divide the subgenus into the following groups by their chaetotaxy:

1. Area Verticalis confluent with Area Occipitalis and provided with only 1+1 setae .... *nivicola* Group
   Area Verticalis is confluent with Area Occipitalis, or not, and always provided with 2+2 setae 2
2. Abd. V with three transverse rows of setae .... *christianseni* Group
   Abd. V with two rows of setae 3
3. S.s. upon Abd. I-III; Abd. IV and Abd. V is p_4, p_4, p_2 in position .... *reticulata* Group
   S.s. upon Abd. I-III; IV and Abd. V is p_5, p_5 and p_3 in position 4
4. Tenent hair 1, 1, 1 .... *manubrialis* Group
   Tenent hair usually 2, 3, 3 .... *viatica* Group

The latter two groups are only provisional and their members must be re-examined.

THE NIVICOLA GROUP

This group is characterized by its having only 1 + 1 setae on the Area Verticalis, which is fused with the Area Occipitalis. Tenent hair 1,1,1 and sensory hairs of Ant. IV usually rod-like. Only the three species here described are known, although there must be more species to be included in this group.

Hypogastrura (*s. str.*) *nivicola* (Fitch)
Figs. 13, 46

Syn. *H. socialis:* Uzel, 1890; Stach, 1949.

The American examples of the species agree with the description of Stach, 1949. P.A.O. with one large accessory tubercle. Dens with seven setae dorsally, normal in position. The inner side of the basal half of the mucro slightly lobed (*cf.* Stach, 1949, p. 76 and Plate IV, Figs. 6-9; not shown in Folsom's 1902 or 1916 figures). Distal end of the dens with a cap-like thickening of the integument on its ventral side (*cf.* Stach, 1949, Plate IV, Figs. 7, 9). Most body setae equally long and simple except on Abd. IV, V, and VI, where some of the larger setae are slightly feathered. Area Verticalis of head not divided from Area Occipitalis and with only 1+1 setae. Th. II-III with m_2 apparently missing; p_4 is s.s. Abd. I-III with most setae of equal length and p_5 is s.s. Abd. IV with setae in three rows; but as m_1 is missing, dorsal group apparently in two rows; p_5 is s.s. p_1 and p_4 slightly longer than others. Abd. V with p_3 s.s.; p_3, and p_5 longer than p_2. Abd VI with all setae long.

Specimens seen.—Four specimens from Peterborough, New Hampshire, USA (14 V 1950, K. Christiansen, collector). Fifteen specimens from Richland (?), Pennsylvania, USA (1 VI 1940, S. W. Frost, collector).

Hypogastrura (*s. str.*) *copiosa* (Folsom)
Figs. 14, 48-53

Folsom, 1916.

Syn: *Achorutes schneideri* Guthrie, 1903 (*nec* Schaffer).

Body length about 1.5 mm. Color brownish black except for ventral side and extremities. Ant. IV with an end-bulb in a deep groove. Sensory setae of the dorsal side short, blunt and rod-like in appearance, about 9 in number. Eyes eight per side, upon black patch. P.A.O. composed of four minute elements in a shallow groove, directly before eyes and about 1/2 to 1/3 of an eye in diameter. Accessory tubercle not mentioned. Third antennal segment organ of two rods without groove and with two guard setae nearby. Ungues of all legs equal, with an inner tooth near apex. Lateral tooth not to be seen. Unguiculus setaceous, half the length of the unguis and with a narrow, rounded basal lamella. Tenent hairs 1, 1, 1, very long and thick, distally not narrowed, and truncate. Ventral tube with four setae per side. Rami of the tenaculum 4-toothed. Dorsal side of dens smooth, with seven long setae. Mucro small, almost straight and only slightly rounded apically. D/Mu as 22:5. Mu/Ung_3 as 5:12. One unclear

outer lobe often seen. Anal spines small, acute, on basally contiguous papillae which are as long as the spines. An.sp./Mu as 7:5. All body setae moderately developed, somewhat stout and blunt (as in *H. viatica*); longer ones slightly serrate; s.s. setaceous. Area Verticalis confluent with Area Occipitalis and with only 1+1 seta as in *H. nivicola.* Th. II, III with setae in three rows. P_4 is s.s. and slightly longer than others. Abd. I-III with setae in three rows. P_5 is s.s. All setae equally long. Abd. IV with setae in three rows and p_5 s.s. Abd. V with setae in two rows, p_3 s.s. and longer than others.

Specimens seen.—Eight specimens from Cochetopa Pass, Colorado, USA (9 VII 1950, K. Christiansen, collector).

Hypogastrura sp. (?)

Syn: *Neogastrura reticulata* Hammer, 1953 (*nec* Börner).

Specimens from the Canadian arctic determined by M. Hammer as *H. reticulata* do not belong to this species. They differ from Japanese specimens identified as *H. reticulata* Börner in not having a well-developed tenent hair on each tibiotarsus. I have received two specimens already mounted in Salmon's fluid from Miss Hammer. As they are in a lateral position and intensely pigmented, I am unable to determine their chaetotaxy. Only the head capsule is available for this purpose, and here I can find the Area Verticalis is fused with the Area Occipitalis and provided with 1+1 setae. In view of this, this species — which I am unable to identify — must be included in the *nivicola* Group.

THE CHRISTIANSENI GROUP

The present group is easily identified by having three rows of body setae upon Abd. V. The group is represented by only two species at present.

H. christianseni n. sp.—All body setae simple; USA.

H. itaya Kinoshita.—Some of the setae on Abd. V and VI are long and distinctly swollen terminally; Japan.

Hypogastrura christianseni n. sp.
Figs. 15, 54-61

Body length 1.5 mm. Color blackish gray. The pigment is in blotches especially dense on the posterior part of the head. Antennae well-pigmented. Ventral side pale. Extremities almost unpigmented. Ant./Head as 1:1. Ratio of antennal segments I-IV as 10:12:13:17. Ant. IV with a terminal bulb in a deep pit accompanied by 2-3 weak setae and 7 well-developed, curving sensory setae. No eversible sac on Ant. III/IV. Third antennal segment organ composed of two small rods in a shallow groove and two modified companion setae. P.A.O. about 1.5 times the diameter of an eye and composed of four subequal elements. Accessory tubercle not found. Leg with one prominent tenent hair ending in a small bulb. Unguis well-developed and with one inner tooth. Unguiculus spiniform and equipped with a very narrow basal lamella, which is not larger than the basal papilla of the ungui-

culus. Ventral tube with 4+4 rather long setae. Rami of the tenaculum with three teeth. Furcula well-developed. D/Mu as 4:1. Mu/Ung_3 as 5:9. The dorsal surface of manubrium with many setae. The dorsal surface of the dens with coarse granules and seven setae situated just as in *H. manubrialis*. Mucro slightly curving and ending in a blunt head. A broad outer lamella runs from the base almost to the end of the mucro. The anal spines are small (although larger than those of *H. manubrialis*) and situated on subequal papillae. The spines are straight and pointed, while the papillae are slightly curved. The length of the spines plus the papillae subequal to Ung_3. Body setae not well-developed. Distinction between Area Frontalis and Area Occipitalis slight. Th. II, III with m_2 missing; p_4 s.s. and longer than others; with a prominent fovea between p_3-p_4. Abd. I-III with setae in two rows; p_5 s.s. and larger than others; with fovea between p_2-p_3 and proximal to p_5. Abd. IV with setae in three rows and almost equal in length. Foveae proximal to p_2, between m_2-m_3 and proximal to p_4, which is slightly larger than others. Abd. V with three rows of setae, m_1 being present; p_3 s.s. and longer than others. Abd. VI with setae in two rows.

This is the only species to have three rows of normal setae on abdominal segment V. In other features and particularly in the form of the mucro, it is akin to *H. manubrialis assimilis* Krausbauer. In one example, anal spines were lacking just as in *H. manubrialis* f. *neglecta* Born, 1900. In this case, an extra pair of setae (p_1) were seen in the position of anal spines, implying that not only the unusual spines of *H. duplicispinosa* Yosii but also the normal anal spines are substantially equivalent to setae located in the same position. The species is named after my colleague, Dr. Kenneth Christiansen.

Holotype.—One male from Palouse, Washington, USA (K. Christiansen, collector).

Paratypes.—Four specimens from the same sample.

Hypogastrura itaya Kinoshita
Figs. 16, 62-68

Kinoshita, 1916.

Body length 1.2 mm. Pigment dark gray or bluish gray. Ventral side pale. Yellowish ground color seen along segmental margins and ventral side. Pigment distributed in patches. Ant./Head as 11:10. The ratio of antennal segments as 10:13:15:18. Ant. IV with a small end-bulb in a shallow groove with three to four socket setae. Sensory setae of dorsal side usually four in number and a little smaller than the normal setae. On the ventral surface near the end-bulb, one prominent, thick seta occurs. Third antennal segment organ normal and companion setae short and well-differentiated. Base of antenna not clearly separated from Area Frontalis. P.A.O. of four small elements. Whole organ is 1.5 times the diameter of one eye. Eyes eight per side upon black patches. Unguis with one inner tooth and often with one pair of lateral teeth. Unguiculus setaceous, half as long as the unguis,

with a small basal lamella. Tibiotarsus with tenent hairs 3, 4, 4 in number, well-developed and apically swollen. One dorsal tenent hair is slightly stronger than the lateral two which are inserted at the same level on the tibiotarsus. Middle and hind legs with an additional extra long tenent hair arising from a higher level of the tibiotarsus. This hair is absent on forelegs. Ventral tube with 4 + 4 setae. Rami of the tenaculum with three teeth. Furca slightly reduced, its apex reaching only to the foremargin of Abd. III. Manubrium with 10 + 10 setae on dorsal side. Dens ventrally smooth and dorsally finely granulated, with five setae, one external-basal seta being extra long. D/Mu as 3:1. Mu/Ung_3 as 4:9. Mucro rather reduced, slightly curved and distally pointed, its outer margin being lamellate, with lobe at about the middle. Anal spines strongly recurved and acute. Basal papillae touching each other at the base and the margins between the papillae and the anal spines are higher in front than in back. An. sp./Ung_3 as 1:3. Entire integument minutely granulated. Body setae not large, slightly thickened and truncate as in *H. viatica*. Area Verticalis confluent with Area Occipitalis and with 2+2 setae. Th. II, III with setae in three rows; p_2 and p_4 longer than others and slightly swollen at apex. Abd. V with setae in three rows; m-row (m_1 and m_2) very large and distally swollen, while those of a- and p-rows are normal. Abd. VI with two rows of setae. P_1 and one lateral seta (p_2?) very long and distally swollen. One other such seta present on the side-lobe of the anus.

Three rows of setae on Abd. V and clavate body hairs are characteristic of the present species.

Specimens seen.—Ten specimens from Mt. Kamuriki, Pref. Nagano (17 VI 1952, S. Ueno, collector); five specimens from Matsumoto, Pref. Nagano (18 VIII 1952, S. Ueno, collector).

THE RETICULATA GROUP

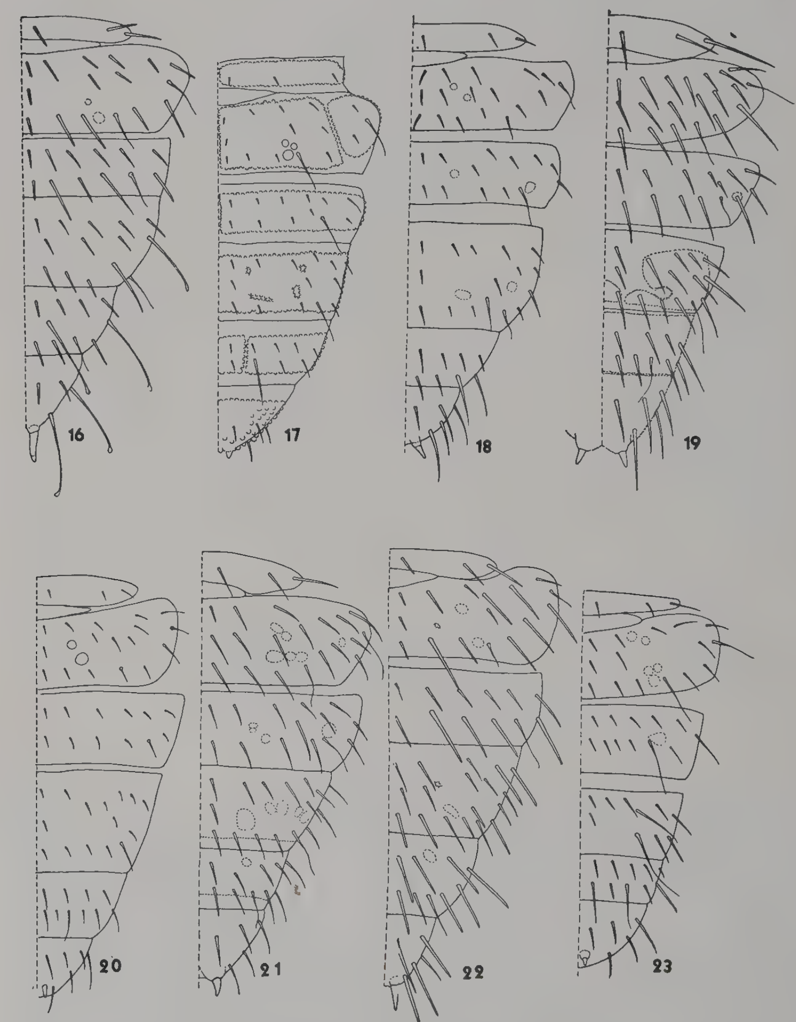
This group is characterized by s.s. assuming the position of p_4, p_4, p_4, p_2 upon Th. II, III, Abd. I-III, Abd. IV and Abd. V respectively. The only known species is *H. reticulata* Börner from Japan.

Hypogastrura reticulata Börner
Figs. 17, 46, 69-73

Börner, 1909.

Body length up to 2.3 mm. Color dark or black. Ant./Head as 25:30. Ratio of antennal segments I-IV as 3:5:5:12. Ant. IV with a small end-bulb in a shallow pit. Sensory setae blunt, rod-shaped, and more than 12 in number. Third antennal segment organ composed of two rods in a groove accompanied by two modified setae. Two additional modified setae are proximal to the latter. Anal antennal segments coarsely granulated. Base of antenna more finely granulated and thus sharply separated from Area Frontalis and Ant. I. Granulations extremely coarse on Area Ocularis. Eight eyes per side. P.A.O. small, with four oval elements in a shallow groove somewhat separated from Area Ocularis. One prominent tenent hair on each tibiotarsus which is not only longer than the unguis and very thick, but also dis-

tally enlarged in a triangular form as in the genus *Entomobrya.* Unguis with one distal inner tooth. Dorsal side strongly carinate; lateral tooth not observed. Unguiculus setaceous, about half as long as unguis and with a broad basal lamella. Ventral tube with 4+4 setae. Rami of the tenaculum with four teeth. Furca well-developed. Manubrium with about six setae dorsally. Dens minutely granulated dorsally and



Figs. 16-23.—16. *Hypogastrura* (*s. str.*) *itaya* Kinoshita. 17. *H.* (*s. str.*) *reticulata* Börner. 18. *H.* (*s. str.*) *manubrialis* (Tullberg). 19. *H.* (*s. str.*) *oregonensis* n. sp. 20. *H.* (*s. str.*) *nemoralis* n. sp. 21. (*s. str.*) *iwamurai* n. sp. 22. *H.* (*s. str.*) *viatica* (Tullberg). 23. *H.* (*s. str.*) *gracilis* (Folsom).

with seven setae including one elongated outer-lateral seta. D/Mu as 10:3. Mu/Ung_3 as 3:5. Mucro almost club-shaped, straight and distally rounded. Both sides of the mucro almost smooth, but sometimes with narrow lamellae, which may reach from the apex to the tip of the dentes or may vanish at about the middle. Anal spines minute, conical in profile, and on papillae which are as high as the spines and are confluent basally. An. sp./Mu as 1:2. Integument coarsely granulated as in *Odontella*. Head with Areas Frontalis and Verticalis coarsely granulated. Setae minute but still normal. One elongated fovea lies in the middle of the Area Frontalis and between t and c. A median band of clearly different granulation extends from the third abdominal segment to the Area Verticalis. Each segment has a coarsely granulated area at about the middle, sharply separated from the more finely granulated areas of the segmental margins. Th. II, III with m_2 apparently absent, only p_4 somewhat longer than the others and with two to three foveae nearby. Abd. I-III with two rows of setae; p_4 long and s.s. while the remaining setae are subequal and small. Abd. IV with setae in three rows; m_2 is apparently absent; a large fovea lateral to m_1 and p_4 very long and s.s. Abd. V with setae in two rows; posterior margin with a distinct finely granulated area; p_2 long and s.s. Abd. VI with setae slightly longer.

Our specimens agree well with the description of Börner, 1909, except for the P.A.O. which is not unilocular, but composed of four elements as usual.

Specimens seen.—The species appears frequently in great numbers in Central Japan during spring and autumn. Thirty specimens from Daimonji, Kyoto (20 XII 1953, R. Yosii, collector) and 18 specimens from Kasuga, Nara (9 III 1952, Y. Wada, collector).

THE MANUBRIALIS GROUP

Almost all species of *Hypogastrura* (s. str.) with 1, 1, 1 tenent hair on the tibiotarsus may be included in this group, although their chaetotaxy must be determined in each case. The position of s.s. upon Th. II, III, Abd. I-III, Abd. IV and Abd V is p_4, p_5 and p_3.

Hypogastrura manubrialis (Tullberg)

Figs. 18, 74-76

Syn. nov. *Achorutes yamagata* Kinoshita, 1916; *A. maturus* Folsom, 1919 (?).

Body length about 1.4 mm. Color grayish brown or bluish. Antennae deeply pigmented. Ventral side and extremities pale. Ant./Head as 1:1. Ant. IV with an extrusible end-bulb in a pit and some socket-setae near by. Sensory hairs in the form of long, somewhat curved rods, eight in number. Third antennal segment organ of two rods in a furrow and two modified setae. Unguis normal, with or without inner tooth about ¾ distance from the base. Unguiculus two-thirds as long as unguis, setaceous, without lamella, but with one basal papilla. Tenent hairs long, 1, 1, 1 and acuminate or slightly knobbed at the end. Ventral tube with 4+4 setae. Rami of the tenaculum with

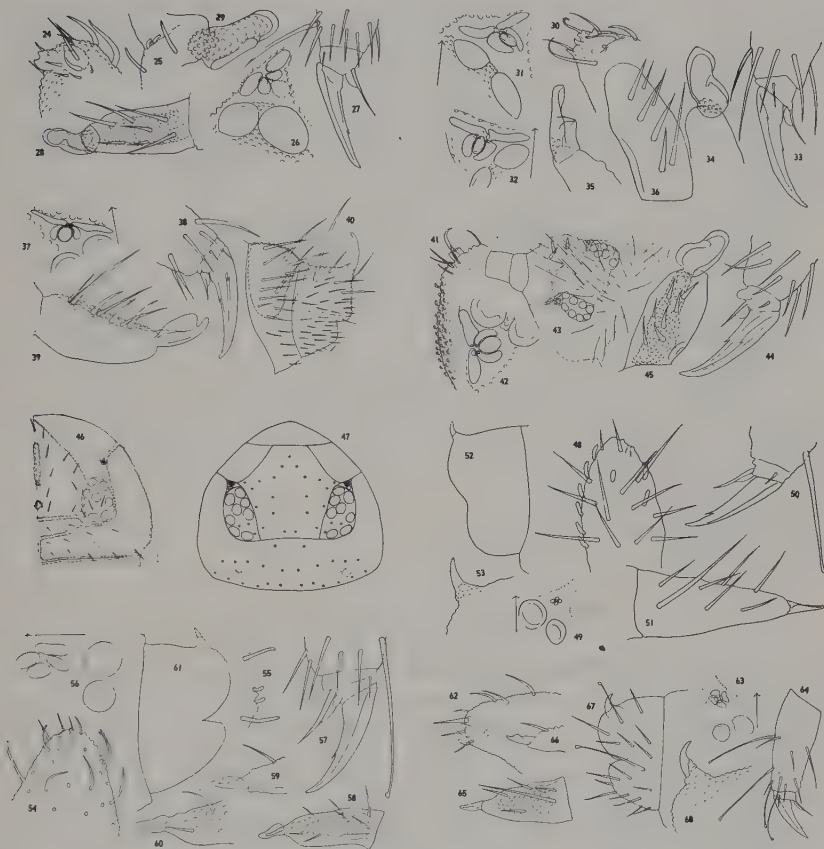
four teeth. Furca normal. Dens/Mu as 5:2. Dorsal surface of dens with coarse granulations and with seven setae including an outer basal seta longer than the others. In all the specimens which were examined, a slight thickening similar to a fold of skin can be seen just before the mucro. This is a diagnostic characteristic of the species. Mucro ventrally almost straight, slightly curved and rounded apically. An inconspicuous, very thin outer lamella is present. Anal spines minute and on small basal confluent papillae. These papillae are about three times as large as the normal skin granules and smaller than half or Ung_3 in length. Body setae poorly developed and often invisible. Head with Area Verticalis confluent with Area Frontalis so that the 2+2 setae on the former seem to be d_1 and sd_1 of the latter. The furrow between Area Verticalis and Area Occipitalis can be either distinct or obscure. A pit lies between c_2 and c_3 as well as between p_3 and p_4. Th. II, III with rather small setae; s.s. not differentiated. Abd. I-III with setae in two rows, those on both sides longer; p_5 is s.s. and longer than all the others.

Specimens seen.—Thirty specimens from Otsu, Shiga Pref., Japan (29 X 1939, R. Yosii, collector); twenty specimens from Point Barrow, Alaska, USA (N. Weber, collector).

Achorutes yamagata Kinoshita from Japan is identical to this species. Material from Point Barrow includes many large and small specimens. Some of the specimens have a mucro of the type seen in *H. assimilis* with a broad lateral lamella and recurved apex. Their tenent hairs are usually clavate. There would seem to be no great difference between the present species and *H. assimilis*. The latter, therefore, cannot be regarded as a separate species.

Hypogastrura nemoralis n. sp.
Figs. 20, 77-83

Body length up to 1.8 mm. Whole body except furca brownish black. Ant./Head as 1:1. Ratio of antennal segments I-IV as 15:20:20:30. Ant. IV with an end-bulb in a shallow pit and some nearby socket hairs. Sensory setae long, somewhat curved, and 8 in number. Third antennal segment organ of two rods in a furrow accompanied by two modified setae. Base of the antenna not differentiated from Area Frontalis. Eyes eight per side. P.A.O. composed of four small elements. Whole organ equal to one eye in diameter. Between P.A.O. and Area Ocularis is a large tubercle which is apparently the accessory tubercle of P.A.O. Each tibiotarsus has one long tenent hair rounded at the tip. Unguis normal with one inner tooth at about the middle. Unguiculus setaceous, about half as long as the unguis and with a prominent, rounded basal lamella. Ventral tube with five setae per side. Rami of the tenaculum 4-toothed. The manubrium has only a few setae. A coarsely granulated area occurs on the dorsal surface of the dens about a quarter of the distance from the apex of the organ. Distal end of the dentes with a cap-like thickening of the integument just as in *H. bengtssoni* (Agren); (*cf.* Stach,



Figs. 24-68.—24-29.—*H.* (*Ceratophysella*) *pseudarmata* (Folsom). 24. Distal end of Ant. IV. 25. Ant. III-organ. 26. Postantennal organ. 27. Hind foot. 28. Dens and mucro (dorsal view). 29. Mucro. 30-36.—*H.* (*Cyclograna*) *vulgaris* n. sp. 30. Distal end of Ant. IV. 31. Postantennal organ. 32. Postantennal organ. 33. Hind foot. 34. Mucro (dorsal view). 35. Mucro (lateral view). 37-40.—*H.* (*Cyclograna*) *loricata* n. sp. 37. Postantennal organ. 38. Hind foot. 39. Dens and mucro. 40. Abd. V and VI (lateral view). 41-45. —*H.* (*Cyclograna*) *horrida* n. sp. 41. Ant. IV. 42. Postantennal organ. 43. Head capsule. 44. Middle foot. 45. Dens and mucro (dorsal view). 46. Chaetotaxy of the head of *H.* (*s. str.*) *reticulata* Börner. 47. Chaetotaxy of the head of *H. nivicola* (Fitch). 48-53.—*H.* (*s. str.*) *copiosa* (Folsom). 48. Ant. IV (dorsal view). 49. Postantennal organ. 50. Middle foot. 51. Dens and mucro (lateral view). 52. Abd. VI (lateral view). 53. Anal spine. 54-61.—*H.* (*s. str.*) *christianseni* n. sp. 54. Distal end of Ant. IV. 55. Ant. III-organ. 56. Postantennal organ. 57. Hind foot. 58. Dens and mucro (dorsal view). 59, 60. Mucro. 61. Abd. VI (lateral view). 62-68.—*H.* (*s. str.*) *itaya* Kinoshita. 62. Distal end of Ant. IV. 63. Postantennal organ. 64. Hind foot. 65. Dens and mucro. 66. Mucro. 67. Abd. VI (lateral view). 68. Anal spine (lateral view).

1940, Pl. XV, 6, 7, 8). Dorsally, there are seven setae. Dens/Mu as 3:1. Mu/Ung_3 as 5:6. Mucro dorsally flattened, ventrally curved, granulated along the shaft, laminate on both sides and with one prominent outer lobe at about one-third of the way from its tip. Anal spines relatively small and located directly upon the abdomen without intermittent anal papillae. An. sp./Mu as 1:5. Integument minutely granulated. Setae small and simple. Upon head, Area Verticalis confluent with Area Occipitalis and with 2+2 setae. Th. II-III with three rows of setae; m-row is well represented and $m_2 = m_1$; s.s. is not differentiated from others. Abd. I-III with two rows of setae. S.s. is p_5 and small. Abd. IV with setae subequal and in three rows; s.s. a little longer than others and p_5 in position. Setae of Abd. V longer but subequal in length. S.s. is p_3. Abd. VI has a_1 and p_1 longer than others.

The species is characterized by the absence of anal papillae and presence of a cap-like structure on the distal end of the dens. The insufficiently known species, *H. thelli* (Tullb.) from Novaya Zemlya resembles the present form.

Holotype.—One male from Mt. Ubasute, Nagano Pref. (17 VI 1952, S. Ueno, collector).

Paratypes.—Nine specimens from the same sample.

Hypogastrura oregonensis n. sp.
Figs. 19, 84-89

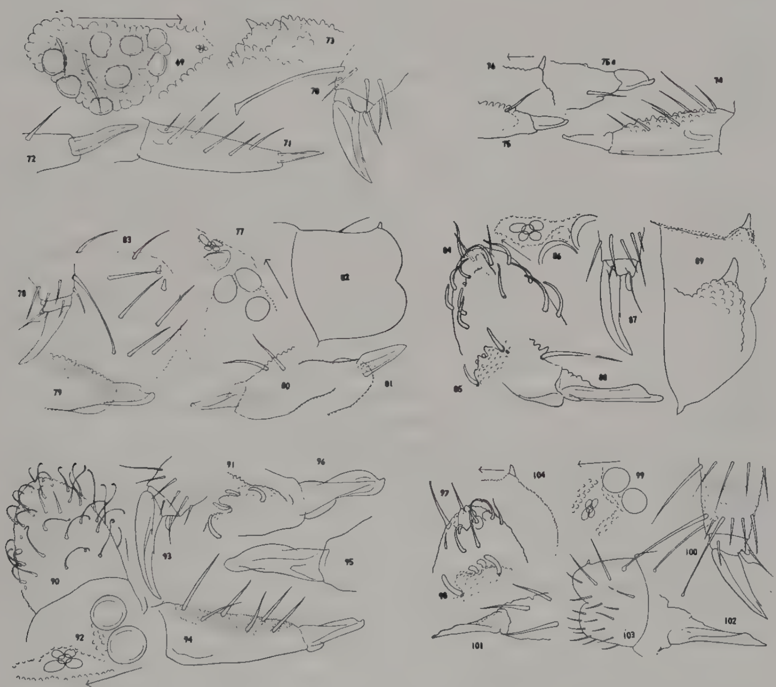
Body length 1.8 mm. Color chestnut brown. Antennae and head somewhat darker than remainder. Ant./Head as 12:10. Ant. IV with an end-bulb in a deep pit and accompanied by some socket-setae. Dorsal sensory setae 7-9, some of them similar to common setae. Eversible antennal sac absent. Third antennal segment organ normal, with two modified companion setae. P.A.O. of four elements; anterior two a little larger than the posterior two. Accessory tubercle not present. Eyes eight per side, upon black patch. Tibiotarsus lacks tenent hairs. Unguis with one inner tooth and a pair of lateral teeth. Unguiculus setaceous and with a very broad, rounded basal lamella. Ventral tube with 4+4 setae. Rami of the tenaculum with four teeth. Furca well-developed. Dens/Mu as 2:3. Dens dorsally coarsely granulated with seven setae. The granulation is more striking directly before the mucro, where the ventral side has a small cap-like thickening of the integument. Mucro laterally compressed and almost bladelike. Distally, there are two obscure teeth. Ventral side strongly carinate, with a small mucronal tunica near the base. Dorsally a small portion near the base is granulated. Anal spines about one quarter as long as the mucro. Basal papilla of the spine rather hemispherical, basally contiguous, and as high as the spines. Body setae simple and well-developed for the genus. All setae of Area Frontalis equally long. Area Verticalis with 2+2 setae and confluent with Area Occipitalis. Th. II, III with setae subequal; p_4 is s.s. Abd. IV with a median, unpaired, coarsely granulated tubercle including p_2 of both sides.

Another lateral tubercle with such a coarse area includes p_3-p_6 and extends anteriorly beyond the a-row. P_5 is s.s. Abd. V and VI coarsely granulated over whole segment. Setae distributed normally.

The characteristic structure of furca, dentes, and mucro and the granulation of Abd. IV make the species at once separable from other members of the group.

Holotype.—One male from Corvallis, Oregon, USA (26 XII 1950, V. Roth, collector).

Paratypes.—Four specimens from the same sample.



Figs. 69-104.—69-73.—*H.* (*s. str.*) *reticulata* Börner. 69. Postantennal organ and eyes. 70. Middle foot. 71. Dens and mucro. 72. Mucro. 73. Anal spines (oblique dorsal view). 74-76.—*H. manubrialis* (Tullberg). 74. Dens and mucro (lateral view). 75, 75a. Mucro. 76. Anal spine. 77-83.—*H. nemoralis* n. sp. 77. Postantennal organ. 78. Hind foot. 79, 80, 81. Dens and mucro. 82. Abd. VI (lateral view). 83. Anal spines (oblique dorsal view). 84-89.—*H. oregonensis* n. sp. 84. Distal end of Ant. IV. 85. Ant. III-organ. 86. Postantennal organ. 87. Fore foot. 88. Mucro. 89. Abd. VI and anal spine (lateral view). 90-96.—*H.* (*s. str.*) *iwamurai* n. sp. 90. Distal end of Ant. IV (dorsal view). 91. Ant. III-organ. 92. Postantennal organ. 93. Fore foot. 94. Dens and mucro. 95, 96. Mucro. 97-104.—*H.* (*s. str.*) *gracilis* (Folsom). 97. Distal end of Ant. IV (ventral view). 98. Ant. III-organ. 99. Postantennal organ. 100. Middle foot. 101, 102. Mucro (lateral view). 103. Abd. VI (lateral view). 104. Anal spine.

Hypogastrura iwamurae n. sp.
Figs. 21, 90-96

Body length up to 2.5 mm. Body somewhat dorso-ventrally flattened as in Ceratrimeria. Ground color ash-gray. Dorsal side of the body and antennae bluish, other extremities pale. Ant./Head as 25:23. Ratio of antennal segments I-IV as 20:20:25:30. Ant. IV with a relatively small end-bulb in a deep groove, accompanied by some socket setae. More than 15 sensory setae on dorsal side, very long and distinctly curled at the apex. Peg-like setae of the ventral side obscure and few in number. Antennal eversible sac absent. Third antennal segment organ composed of two small rods in a shallow groove and two accessory setae. The latter are somewhat curved and apparently modified. Antennal segments I and II pale and with one row of setae. Granulations of the antennal bases distinctly finer than remainder of head. P.A.O. composed of four elements in a deep furrow. Whole organ about equal to one eye in diameter. Accessory tubercle not seen. Eyes eight per side, upon a black eye-patch. Area Verticalis confluent with Area Occipitalis with 2+2 setae. Unguis strongly keeled dorsally and with one central inner tooth. A pair of lateral teeth present. Unguiculus setaceous, about half as long as unguis, with a small rounded basal lamella, slightly longer than the granulated basal papilla nearby. One feeble tenent hair present on all legs, similar to normal setae. Ventral tube with 4+4 small setae. Rami of the tenaculum quadridentate. Furca well-developed. Dens/Mu as 7:3. Dentes distally slightly convergent, ventrally smooth and dorsally granulated from the base until shortly before the apex. Six unthickened dental setae. Form of mucro complicated, strongly carinate ventrally and with one obvious inner tooth near the base. Distal end of mucro rounded and with a lateral lamella on each side along its distal two-thirds. In profile, these hyaline lamellae are invisible. Anal horns short, thick, slightly curved, with anal papillae as long as the anal spine and contiguous basally. Often the spine reveals some surface ringing. Anal spines (minus papillae) to the mucro as 1:2. Mu/Ung_3 as 15:23. Granulations of the integument very coarse. Along the posterior margin of Abd. IV and V, there are a number of sharply delimited, finely granulated areas. Body setae long, simple and acuminate. The positions of s.s. on each of the body segments are as 0, 4, 4, 5, 5, 5, 5, 3, 0 in a posterior row. They are all subequal to the body setae.

This species is remarkable in the form of the mucro, and the sensory setae of the fourth antennal segment. The species name is dedicated to my friend, Michimasa Iwamura of Saikyo University.

Holotype.—One male from Asiu, Kyoto Pref., Japan (30 X 1937, M. Iwamura, collector).

Paratypes.—Three specimens from the same sample; fifteen specimens from Hyonosen, Hyogo Pref. Japan (28 VIII 1938, R. Yosii, collector); one specimen from Shizugadake, Shiga Pref., Japan (14 IX 1938, R. Yosii, collector).

THE VIATICA GROUP

This group includes those species which usually have 2, 3, 3 tenent hairs on the tibiotarsus. Position of s.s. is normal.

Hypogastrura viatica (Tullberg)
Fig. 22

Tullberg, 1872; Stach, 1947.

Distribution of setae on head normal. Antennal bases undifferentiated. Area Verticalis confluent with Area Occipitalis and with 2+2 setae; v_1, v_2. Th. II, III with small fovea near m_2 (lat.); s.s. is at the position of p_4. Abd. I-III with two rows of setae; a fovea between p_2-p_3; p_5 is s.s.; Abd. IV with setae in three rows; a small fovea near m_2 (lat.); s.s. at the position of either p_3 or p_5, which are needle-shaped and subequal in form. Abd. V with setae in two rows. S.s. is p_3. The body setae show much variety in shape and length. Longer setae truncate and often serrate distally (*see* Stach, 1949); other setae small, simply needle-like in appearance. Dentes with six setae. Ventral tube with 4+4 hairs. Rami of the tenaculum tridentate.

Specimens seen.—Twenty-five examples from Liège, Belgium (F. Carpentier, collector).

Hypogastrura gracilis (Folsom)
Figs. 23, 97-103

Achorutes gracilis Folsom, 1899.

Achorutes tullbergi Schaffer, 1900, syn. nov. (?)

Body length 1.5 mm. Color black to blue black. Antennae deeply pigmented. Ventral side and other extremities pale. Ant./Head as 10:9. Ratio of antennal segments I-IV as 12:13:18:30. Fourth antennal segment with a distal, trilobed end-bulb and a number of socket-setae. No peg-like setae on ventral side. Third antennal segment organ of two small rods in a shallow groove accompanied by two curved setae. P.A.O. small (about as large as one eye) composed of four minute, subequal elements. Accessory tubercle not seen. Eyes eight per side, upon black patches. Unguis of all legs subequal, relatively small, dorsally carinate and with one inner tooth near the distal end of each. Unguiculus setaceous and reaching three-quarters of the distance from base to apex of unguis. Basal half lamellated on the inner side with lamella apically arcuate ("lunate" of Folsom). Tenent hairs 2, 3, 3 rather thick and conspicuously swollen at apex; all of a given leg arise from the same level with the median seta slightly larger than others on mid- and hind legs. Dens/Mu as 3:1. Dentes almost smooth dorsally with seven setae. Mucro strongly compressed bilaterally and therefore somewhat blade-shaped. Apical tooth pointed, but anteapical tooth obscure and often absent. Mucro lamellate on both sides from the base to the anteapical tooth. Inner lamella not as conspicuous as outer one. Mu/Ung_3 as 10:11. Anal spine small and located on anal papilla as high as the spine itself and separated basally. Mu/An.sp. as 10:3. Integument minutely granulated. Body setae all very minute. Head with Area Verticalis confluent with Area Occipi-

talis and with 2+2 setae. Th. II, III with almost all setae equally long; p_4 is s.s. and a little longer than others. Abd. I-III: p_5 is s.s. about twice as long as other setae and located on the dorsal side of conspicuous fovea. Chaetotaxy of Abd. IV difficult to observe. At any rate, p_5 is s.s. and longer than others. Abd. V with setae in two rows; p_2 is smaller than p_1, and s.s. p_3.

The present species is very near to *H. tullbergi* Schaffer, 1900. The main difference is the shape of unguicular lamellae, which are arcuate in *gracilis* and rounded in *tullbergi.* It is by no means constant in form and I have found some examples with rounded lamellae and some intermediate forms between these extremes.

Specimens seen.—Thirteen specimens from the seashore near Hiroshima (Y. Taki, collector).

CONCLUSIONS

The crucial characteristic for separating *Ceratophysella* from *Hypogastrura* is the position of s.s. upon Th. II and III, and not the presence of an eversible antennal sac. With the former criterion it is possible to include in the genus cavernicolous forms such as *H. cavicola, H. troglodytes,* and *H. quinqueoculata,* all of which are obviously closely allied to *C. armata.*

Those species close to *Ceratophysella,* but having a peculiar P.A.O. form, and with s.s at the position of p_4 on the second and third thoracic segments are placed in the new subgenus *Cyclograna.* The members of this group exhibit a marked tendency toward "plurichaetosis" and "polychaetosis." Frequently some of the setae of the body are spine-like.

It is quite possible that all the forms here discussed are evolved from three species: *C. armata, C. communis,* and *C. vulgaris.* In terms of distribution these forms are European, Eastern Asiatic, and North American, respectively. Where they have given rise to cavernicolous forms, a number of troglobiontic species (*troglodytes, cavicola,* etc.) and even genera (*Typhlogastrura, Spelogastrura,* etc.) appear.

Hypogastrura (s. str.) is relatively difficult to subdivide and, except for the *nivicola* group, will require further study before any natural arrangement can be achieved.

ADDENDUM

Professor H. G. James of the Entomological Laboratory, Dept. of Agriculture in Belleville, Ontario, Canada, has kindly let me investigate the hypogastruran materials of his collection. With many thanks, I should like to note the results as follows:

Ceratophysella armata (Nicolet)

Many specimens from Geraldton, Ontario, Canada (12 IX 1933).

Many specimens from New Westminster, British Columbia, Canada (7 I 1949).

Ceratophysella communis (Folsom)

One specimen from Lampart House, Northwest Territories, Canada (20 VIII 1951).

One specimen from Rondeau Park, Ontario, Canada (2 X 1931).

Ten specimens from Pottageville, Ontario, Canada (3 IV 1931).

Cyclograna vulgaris Yosii

Five specimens from Boyer, Oregon, USA (27 IV 1934).

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The Physiology of Hunger in the Blowfly[1]

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The behavior of an animal typically changes as a consequence of feeding and starvation, at least those aspects of its behavior that are adapted to the location and ingestion of food. The physiological basis of such changes has been long sought by vertebrate psychophysiologists, but the underlying mechanisms are still notably obscure. Of animals with simpler or more stereotyped behavior, similar questions have rarely been asked. Owing much to its usefulness in the study of chemoreceptor mechanisms, the blowfly is recently an exception. There have been a number of investigations directed at the mechanisms whereby feeding alters taste sensitivity, readiness to feed, control of intake, locomotor activity, and other behavior in addition to the abundant information regarding the properties of chemoreceptors as they are involved in feeding.

We have continued that line of investigation to fill in some of the gaps in the simple, rather thorough picture that has resulted. This paper gives the new evidence we have obtained (referred to herein as Evans and Barton Browne, unpublished), and attempts at the same time to evaluate other pertinent evidence and to present an integrated description of the physiology of hunger in the blowfly.

The use of the word "hunger" in the title requires some comment. It has been used there merely to connote those changes in behavior which are a consequence of feeding and starvation. The term has been avoided elsewhere in this paper in recognition of the difficulties engendered by its use. These difficulties are discussed later in order to make use of the experimental data in that discussion.

Feeding Behavior

In examining the effects of feeding and starvation on the feeding behavior of blowflies, we will consider first the effects on the behavioral threshold of the tarsal contact chemoreceptors and then, using the available data, we will discuss the mechanisms whereby ingestion is controlled. A discussion of the phenomenon of "hyperphagia," reported by Dethier and Bodenstein (1958), is also included.

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TASTE THRESHOLD

Feeding is known to decrease the sensitivity of flies to chemical stimulation in two ways. A short-term elevation of threshold is due to sensory adaptation, which Dethier (1952) has shown to be of two types, central and peripheral. Stimulation of a single chemoreceptor hair by a sugar solution soon adapts that receptor to the test solution but does not affect the response of other hairs to stimulation. When, however, many hairs are stimulated at once and for a prolonged period, the response to stimulation of still other hairs is blocked by adaptation of common elements farther along the reflex pathway. In addition, there is a long-term effect on the taste threshold caused by some action of the food after ingestion (Evans and Dethier, 1957).

We will deal mainly with this latter aspect.

MEASUREMENT OF THRESHOLDS

The usual method of threshold measurement, that which was introduced by Dethier and Chadwick (1947, 1948), consists of determining the concentration of the test substance to which 50 per cent of a population of 120 flies exhibit a feeding response, i.e., extension of the proboscis. Two such thresholds generally must differ by threefold for significance at the one per cent level.

In order to work with smaller populations, we have devised a new method of treating tarsal thresholds. It can replace the usual methods only in those cases where a comparison of two or more thresholds on the same fly is part of the experimental design. Herein, we have used it to test the effect of some experimental treatment on the tarsal threshold to a given sugar. It can be used equally well to compare quantitatively the sensitivity of a group of flies to two or more compounds. While retaining the variability inherent in repeated tests on an individual, the method compensates for the variability among the members of the population, and thereby gives reliable results with fewer individuals. Ascending thresholds are obtained for individual flies, beginning at a concentration low enough that none of the flies will respond. After treatment another threshold is obtained for the same flies, beginning at the same low concentration. Since the series of test solutions is arranged as usual in doubling concentration steps, the second threshold of a fly must equal the first threshold $\times\ 2^n$ where n is necessarily a whole number. To allow statistical treatment of cases where there is either no change in threshold or a decrease, the exponent is taken as the measure of threshold change. Thus, a negative exponent indicates a decrease; zero, no change; and a positive exponent, an increase. When a threshold is so high that no response occurs to a nearly saturated solution, e.g. 2 M glucose, it sometimes may be taken as being the next higher doubling concentration (4 M). The practice obviates discarding flies with the highest thresholds when the threshold obviously is high because of the treatment, and, if anything, errs in the direction of smaller-than-real differences. The mean value obtained

for the several flies may now be tested for the significance of difference from zero (e.g. Ostle, 1954); or two groups of flies may be given different treatments and the significance of the threshold changes compared in the two groups. Since significant results have been obtained with as few as 12 individuals, surgical or other laborious procedures are feasible as they would not be for populations of 120 flies.

CHANGES IN TASTE THRESHOLD AFTER FEEDING

The sensitivity of tarsal chemoreceptors to sugar (by behavioral test) is a function of the period of food deprivation; Figure 1 shows the glucose threshold measured as a function of time after a single ingestion of each of four sugars. The plots were made from the data of Evans and Dethier (1957). Curves of the same shape are obtained when fucose is used to measure threshold, but all threshold values are lower because fucose is slightly more stimulating than glucose (Hasset *et al.,* 1950). Fucose and glucose are highly stimulating to the tarsal and labellar chemoreceptors, mannose is weakly so, and lactose not at all. Fucose and lactose are not utilized by *Phormia* whereas mannose and glucose are excellent nutrients (Hasset *et al.,* 1950). Hence the ingestion of a sugar which is either non-stimulating, non-utilized, or both, is capable of elevating taste thresholds for some time after feeding. Arab (1957) has demonstrated that the sucrose thresholds of the labellar hairs individually and of the labellum as a whole are similar functions of feeding and starvation. Thus, it is probable that all of the external contact chemoreceptors which are involved in feeding behave similarly to one another in this respect. It should be noted, however, that the responses of the several chemoreceptor systems to less common sugars are not necessarily even of the same modality (Dethier *et al.,* 1956).

The early time-course of threshold elevation after feeding has been studied by Evans and Barton Browne (unpublished). Tarsal thresholds to glucose were determined 15, 25, and 45 minutes after feeding 2 M glucose. The 15 and 45 minute thresholds were not significantly different ($p > 0.5$; mean n_{15}-n_{45} $= -0.2 \pm 0.35$); but the threshold was less at 25 than at 45 minutes ($p < 0.01$; mean n_{45}-n_{25} $= 1.17 \pm 0.35$). This observation suggests that disadaptation (central and/or peripheral) is not complete by 15 minutes, contrary to the view of Evans and Dethier (1957).

THE EFFECTS OF THE VOLUME AND THE CONCENTRATION INGESTED ON THRESHOLD

Figure 1 shows that threshold changes are a function of the kind of sugar ingested. Evans and Barton Browne (unpublished) have examined the effect of altering the volume and the concentration of the solution ingested. Predetermined volumes of a sugar solution were transferred to a glass slide from a micropipette; a fly, mounted on a waxed stick by its wings, was allowed to feed on such a drop until a

TABLE I.—Tarsal thresholds to glucose after ingestion of fixed volumes and concentrations of glucose

Solution ingested	Mean initial threshold M glucose	n 15 minutes after feeding Mean ± S.E.	n 45 minutes after feeding Mean ± S.E.	Significance P
10 μl 2 M glucose	0.135	3.5 ± 1.45	3.9 ± 1.24	
				) < 0.01
3 μl 2 M glucose	0.175	1.8 ± 2.04	1.7 ± 1.57	
				) < 0.01
3 μl 0.1 M glucose	0.238	0.2 ± 1.14	–0.3 ± 1.16	

negligible amount was left on the slide. Table I shows that 3 μl of 2 M glucose raised the threshold significantly at both 15 and 45 minutes after feeding while 3 μl of the 0.1 M solution did not. Ten μl of 2 M raised the threshold by a significantly greater amount than did 3 μl of the same concentration. Thus, both volume and concentration of the ingested solution by some mechanism influenced the level to which taste threshold was elevated.

THE EFFECT OF THE INGESTION OF PROTEINACEOUS FOODS ON TASTE THRESHOLD

Blowflies readily feed on meat and other proteinaceous materials. Evans and Barton Browne (unpublished) have examined the effect of the ingestion of liver on taste threshold to glucose. The glucose thresholds of flies which had been allowed to feed to repletion on whole liver for 30 minutes were tested an hour after the termination of feeding. Their thresholds were found to be as high (mean threshold of 18 flies was 2.7 M) as those of flies fed to repletion on 2 M glucose (Fig. 1).

THE CONTROL OF THRESHOLD

The action of the sugar solution on the external chemoreceptors (i.e., adaptation) is too brief to account for the prolonged elevation of threshold after feeding (Evans and Dethier, 1957). Nor, as Dethier and Bodenstein (1958) have shown, does the mere performance of the ingestive act affect thresholds to sugars. Thus, the threshold-elevating action of the ingested solution must be internal. All but a small volume of an ingested solution is diverted into the crop. A constriction of the crop duct near its orifice into the esophagus and peristaltic waves toward the crop contain the sugar solution in the crop. For several days after ingestion of a concentrated solution of a "sweet" sugar to satiety, the crop duct and cardiac valve periodically act in unison to pass a discrete "slug" from the crop to the midgut, where absorption takes place. This transfer is very rapid and occurs with little if any loss of the solution in the esophagus.

Two alternatives, the first, that the ingested solution acts after absorption, and the second that it acts in some region of the gut, have been extensively explored. The evidence which favors the second pos-

sibility will now be presented and the possibility of a hormonal link in the chain of events leading to elevation of the threshold will be evaluated.

Action after absorption.—The immediate result of the absorption of sugars from the gut is an increase in the concentration of sugar in the blood. In the case of utilizable sugars, this is accompanied by a change in the metabolic state of the tissues as the sugar is taken up from the blood. The fact that feeding on fucose and lactose, which are not utilized, causes flies to become less responsive to sugars, argues strongly against any possibility that the metabolic state of the tissues has any influence on taste thresholds.

Evans and Dethier (1957) determined sugar concentrations in the blood of flies after feeding and found no consistent relationship between the taste threshold and either the total blood sugar or the concentration of any single sugar. They also found that injection of large amounts of sugar into the haemocoels of starved flies had no effect upon taste thresholds. Under more natural circumstances blood sugar and threshold were again dissociated; Evans and Dethier (1957) found that blood sugar levels increased during a recuperation period following prolonged flight, although the threshold remained low. In view of these several unsuccessful attempts to demonstrate an action of sugar after absorption, it seems very likely that the threshold-regulating mechanism is located in some region of the gut.

Action in the digestive tract.—Since the crop empties over a period of days (Evans and Dethier, 1957), the sugar solution is present in the digestive tract for a period similar to the period of threshold elevation (Fig. 1). However, a number of experiments eliminate the crop itself as the site of action. When crop volume was plotted against glucose threshold for each of the sugars tested, no consistent relationship was apparent (Barton Browne and Evans, 1960). More directly, ligation of the crop duct (Evans and Dethier, 1957), or even removal of the crop (Dethier and Bodenstein, 1958), did not prevent threshold elevation although the period of elevation was diminished. The volume ingested was, of course, much less after ligation of the crop duct, and ligation of the duct after feeding left only a small volume of the ingested solution in the foregut and midgut. It seems unlikely that these small amounts of sugars would remain long in the digestive tract of otherwise starved flies; but threshold remained elevated for 4 hours or slightly longer, an observation which may indicate a lag in the decline of the threshold after the gut is empty. Introduction of sugar into the midgut by injection or by enema did not elevate the threshold (Dethier and Bodenstein, 1958). Hence, these regions do not appear to be involved. Furthermore, these experiments constitute additional evidence against an internal action of sugar, since they must have duplicated at least qualitatively most of the effects of feeding, everywhere but in the foregut. Again pointing to the foregut as the site of action was the demonstration that a ligature just behind

the proventriculus did not prevent threshold elevation when a sugar solution was fed (Dethier and Bodenstein, 1958). All of the above results argue, largely by the elimination of other possibilities, that the threshold-regulating mechanism is located in the foregut exclusive of the crop. From other evidence, Arab (1957) has postulated the existence in the foregut of chemoreceptors which could possibly be involved.

One direct test of the involvement of the foregut has been reported: Dethier and Bodenstein (1958) cut the recurrent nerve just anterior to the corpus cardiacum and by so doing produced "hyperphagic" flies. This result was interpreted to mean that severing the innervation of the foregut via the recurrent nerve interrupted the neural pathway of foregut receptors, the response of which to ingested solutions normally elevates taste thresholds. Unpublished experiments by Evans and Barton Browne that do not support this interpretation are discussed below, together with other aspects of the problem of "hyperphagia." At this stage we regard the relation between input via the recurrent nerve and taste threshold as not satisfactorily demonstrated.

For convenience, we have stated throughout that the ingestion of sugar solutions elevates taste thresholds. This usage, however, ignores the possibility that it may be the absence of solutions in the foregut which causes a sensory input (as, for example, the hunger contractions of the human stomach). If cutting the recurrent nerve does not prevent threshold elevation, then there does not seem to be any compelling reason to prefer the one hypothesis to the other. The input from the foregut might therefore be inhibitory or excitatory in the central nervous system and might be evoked by either the presence or the absence of solutions.

The possibility of a hormonal link.—Two characteristics of the time course of taste threshold after feeding suggest that there may be a hormonal link in the chain of events causing threshold elevation. First, there is the slow attainment of peak threshold. There is a lag of between one and six hours, depending on the sugar used (Fig. 1). Secondly, there is the surprisingly long period of threshold elevation which occurs after feeding of flies, the crops of which have been well ligated or removed (discussed above). Also, de Wilde (1958) has shown that the corpus allatum is intimately involved in the feeding behavior of the Colorado potato beetle. Dethier and Bodenstein (1958) reported that the transfer of diluted blood from fed to starved flies, and the reverse, had no effect on taste threshold. This result argues against the existence of a hormonal link but must be treated with reservation, since any hormone present would have been diluted.

Conclusions.—The relationship between feeding and taste threshold may be summarized by saying that the ingestion of sugars and liver elevates the taste threshold and that the site of action of these substances on the threshold-controlling mechanism appears to be in

the foregut. The actual mechanism involved, however, remains virtually unknown.

THE CONTROL OF INGESTION

The act of feeding in the blowfly may be discussed in terms of a sequence of events: feeding is initiated, maintained, and terminated. It proceeds at a certain rate. This rate and the duration of feeding determine the quantity of food ingested.

INITIATION OF FEEDING

Initiation of feeding involves extension of the proboscis, spreading of the labellar lobes, and the commencement of sucking. All three processes may be elicited by the application of an adequate, acceptable stimulus to one or more of the tarsal or labellar chemosensory hairs. This may be demonstrated by stimulating tarsal or labellar hairs in a way that prevents ingestion of the test solution; under these conditions a fly, dissected to expose its foregut, may be observed to swallow bubbles of air. Normally, however, other sets of receptors are also involved. Spreading of the labellar lobes brings the interpseudotracheal papillae into contact with the stimulating solution. These, like the other contact chemoreceptors, influence feeding. While the tarsal and labellar hairs appear to have the same spectrum of acceptable and unacceptable compounds and a similar threshold (Arab, 1957), evidence has been presented that the papillae reject some compounds that are acceptable for the hairs and have lower thresholds for others than do the hairs (Dethier *et al.*, 1956). In addition, there are indications that

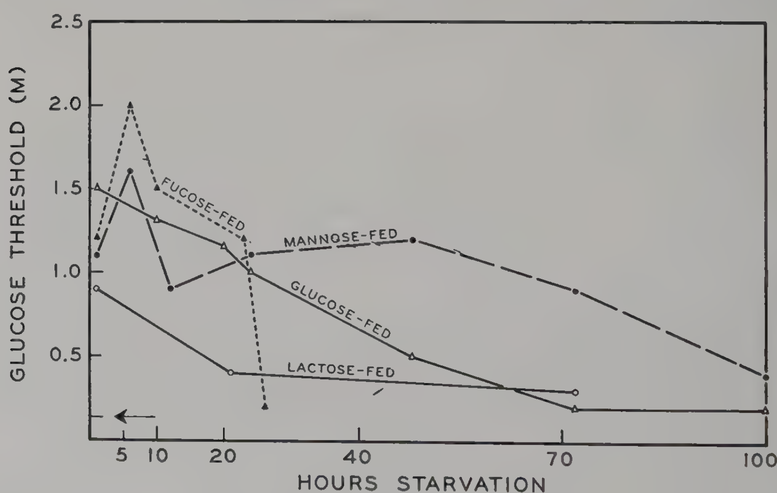

Fig. 1.—The effect of a single feeding on each of four sugars upon subsequent tarsal thresholds to glucose. The arrow indicates the average pre-feeding threshold to glucose (data of Evans and Dethier, 1957).

chemoreceptors, located in the pharynx or esophagus, also monitor injection (Arab, 1957). Feeding is a function of the kind and quantity of input of all these receptor populations.

Only water and some carbohydrates among the pure compounds tested have proven to be acceptable stimuli. A variety of chemically complex, natural foodstuffs are acceptable, but the chemicals responsible are unknown. Bending of the chemosensory hair in extreme starvation can evoke extension of the proboscis; this response has been shown to be mediated by a mechanoreceptor neurone associated with the hair socket (Wolbarsht and Dethier, 1958).

The odor of some foodstuffs attracts blowflies, but the effect of these odors on proboscis extension and ingestion has been little studied. While beef liver is readily ingested by *Phormia,* its odor seems unimportant. Evans and Barton Browne (unpublished) observed that tarsal contact was necessary to elicit proboscis extension and that the response was unaffected by removal of the antennae and palps, which are known to bear the principal olfactory receptors (Dethier, 1954).

CONTROL OF THE AMOUNT OF FOOD INGESTED

Duration of feeding.—The duration of active ingestion of a solution appears to be a function of the stimulating effectiveness of the solution and of the taste threshold of the fly. The duration of feeding is greater on the higher concentrations of a given sugar (Dethier *et al.,* 1956), concentrations which naturally are more stimulating. Evans and Barton Browne (unpublished) have demonstrated, in two experiments, that a relationship exists between the taste threshold and the duration of feeding. Flies were fed to repletion on 0.1 M sucrose solution and were then starved. At intervals from 24 to 72 hours after feeding, batches of these flies were fed 1 M sucrose solution and the

TABLE II.—Duration of feeding on 1 M sucrose as a function of starvation

Hours starvation	Duration of feeding (sec.) Mean ± S.E.
24	51 ± 4.2
36	66 ± 4.8
48	72 ± 3.0
60	86 ± 1.6
72	133 ± 7.9

TABLE III.—Feeding duration on 2 M glucose after ingestion of 2 M glucose and 2 M mannose

Treatment	No. of flies	Feeding duration (sec.) 1 hour after feeding Mean ± S.E.	Feeding duration (sec.) 3 or 4 hours after feeding Mean ± S.E.	Significance *P*
Glucose-fed	29	5 ± 0.53	19 ± 3.3	< 0.001
	26	9 ± 1.3	35 ± 3.1	< 0.001
Mannose-fed	44	5 ± 0.2	4.0 ± 0.4	> 0.05

duration of feeding recorded. Table II shows that the duration of feeding increased with the period of starvation. In the second experiment flies were fed to repletion on 2 M glucose or 2 M mannose. The flies fed 2 M glucose were again fed this solution 1 hour and 3 hours after the initial feeding and the durations were measured. The flies fed the mannose solution were similarly tested with 2 M glucose 1 and 4 hours after the initial feeding. Table III shows that the feeding durations were roughly correlated (negatively) with the taste thresholds shown in Figure 1 for flies fed on these sugar solutions. For flies fed on 2 M glucose the taste threshold decreases in the time interval between 1 and 3 hours after feeding, and it was found that the feeding duration increased during this period. The taste thresholds of flies fed 2 M mannose increased between 1 and 4 hours. Duration of feeding for flies fed on this sugar remained about the same during this period and perhaps even decreased slightly. The observation of Dethier *el al.* (1956) that ligation of the crop duct does not affect the duration of feeding excludes the possibility that gut capacity plays any part.

On the basis of these observations Dethier *et al.* (1956) postulated that an adequate, acceptable chemosensory input is necessary to maintain the sucking response and that ingestion continues as long as the solution tastes "sweet", i.e., until peripheral and central adaptation proceed to a level which renders the solution effectively tasteless. This view does account for the data, and the data exclude a number of other possibilities. The only assumption required is that adaptation to a given level takes longer with more intense stimuli, and this, of course, is quite generally true of sense organs. Implicit in the concept of a threshold-regulating mechanism is that it act somewhere along the reflex chain for proboscis extension in an appropriate manner; such an action would necessarily add with adaptation.

Rate of intake.—The mean rate of intake of sugar solutions has been calculated from measurements of intake volume and duration (Dethier *et al.,* 1956). Generally, rate appears related to the "sweetness" of the solution, to the quantity of acceptable chemosensory input. Sensory input, wherever it has been examined, tends to follow the Weber-Fechner rule, the magnitude of response being proportional to the logarithm of stimulus intensity (e.g. Granit, 1955). Typically, deviations occur at extreme intensities where response increases less rapidly with intensity. The behavioral data of Dethier and Rhoades (1954) show that the Weber fraction (just-noticeable-differences) of preference for sugar solutions by *Phormia* exhibits the typical U-shaped relationship to concentration (Fig. 2). And electrophysiological studies in progress (Evans, unpublished) demonstrated that single chemoreceptor neurones in the hairs exhibit the familiar stimulus intensity-response relationship; a plot of initial frequency of response against log concentration is sigmoid with a long linear segment at intermediate concentrations. The few rate measurements available (Dethier *et al.,* 1956) are in accord with this view; rate of intake increases uniformly with log concentration and declines at near-saturated

concentrations. This, however, cannot be the whole explanation, for rate in certain cases is actually less at the highest concentration than at some lower concentration. Another factor must be involved at the highest concentrations.

Viscosity is one obvious possibility, since concentrated solutions of sugars are notably viscous. The viscosity of sucrose solutions does vary in a way that is roughly appropriate (Fig. 2; data calculated from Bates *et al.*, 1942); viscosity increases rapidly at about 1 M, the concentration at which ingestion rate begins to decline. Dethier *et al.* (1956) demonstrated that viscosity does, in fact, have an effect on the rate of intake. Glycerol, which is tasteless for the blowfly, or nearly so, when added to sucrose solutions markedly decreased the rate of intake but did not affect duration. The rate of intake of a glycerol — 1 M sucrose solution with a viscosity of approximately 50 cp was slightly less than on a 2 M sucrose solution which has a similar viscosity and is slightly more stimulating than the 1 M solution.

Back pressure from the crop or abdomen probably does not normally play a significant part in hindering intake. Normal flies take in about half as much as do the "hyperphagic" flies, the feeding of which is discussed below.

The volume intake of beef liver.—Evans and Barton Browne (unpublished) determined the weights of the crops of flies which had been

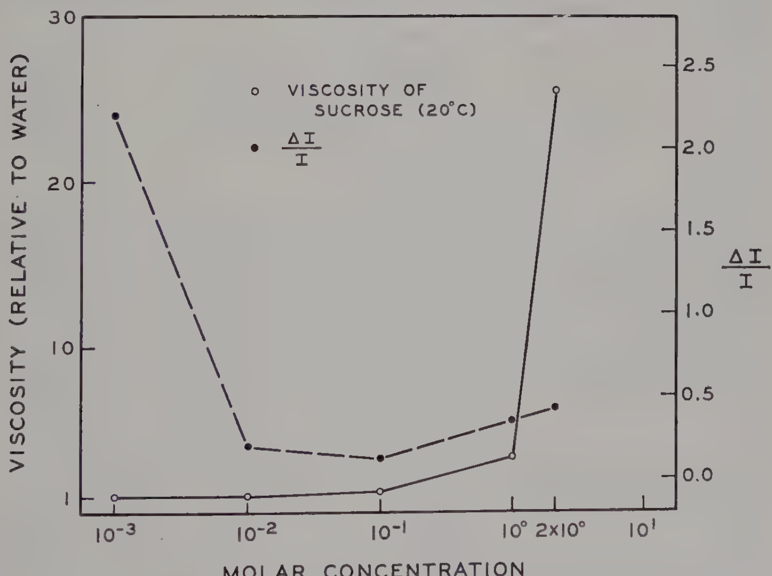

Fig. 2.—Continuous line: viscosity of sucrose solutions as a function of concentration (calculated from data in Bates *et al.*, 1942). Dashed line: ability of the blowfly to detect concentration differences as a function of concentration (data of Dethier and Rhoades, 1954).

allowed access to fresh, whole liver for 1 hour. The mean crop weight was found to be 25 mg. This compares favorably with the crop weight of flies allowed to feed under similar conditions on highly stimulating sugar solutions such as 2 M glucose. In addition, it was found that removal of the antennae and palps did not reduce the intake of liver. Liver appears, therefore, to be highly stimulating for at least one of the contact chemoreceptor systems; removal of the principal olfactory receptors did not markedly influence intake. The intake is almost certainly higher than would be expected if the mono- and oligosaccharide content of the liver were solely responsible and is taken as evidence that other components of liver, not yet tested in pure form, are stimulating to the contact chemoreceptors. The finding that flies which have been fully adapted to liver will respond to 1 M sucrose and that the reverse is not the case shows that the tarsal receptors are less stimulated than would be expected from the volume intake and indicated that other contact receptors, therefore, are more responsive.

Intake of sugar solutions after removal of antennae.—A number of investigators have reported experiments which seem to indicate inhibitory effects (possibly spontaneous) of receptor-bearing structures. Removal of palps or antennae released some activity as if they normally were active and inhibitory. Dethier (1953), for example, has shown that extirpation of the olfactory receptors of lepidopterous larvae increases the number of plant species upon which they would feed. Feeding duration and intake, however, of 2 M glucose were not affected by antennectomy (Table IV). This result was to be expected, in view of the demonstration by Dethier and Chadwick (1947) that antennectomy and labellectomy did not alter tarsal taste thresholds to sucrose and in view of the relation, which is discussed above, that exists between tarsal thresholds and intake.

Conclusion.—Rather surprisingly, the considerable data on ingestion by the blowfly can be explained without departing from familiar neurophysiological concepts. Receptor and synaptic adaptation, stimulus-response relationships, and other properties of receptors and neurones account for most of this rather complex, though stereotyped, behavior. Quantitative predictions regarding ingestion under normal conditions can be made merely from a knowledge of the properties of the test solution and the taste threshold of the fly.

TABLE IV.—Effect of antennectomy on ingestion of 2 M glucose

	Crop weight (mg) Mean ± S.E.		Feeding duration (sec.) Mean ± S.E.	
Normal	15.6 ± 2.0	) $P > 0.4$	58.7 ± 7.3	) $P > 0.1$
Antenna-less	18.0 ± 2.5		77.0 ± 11	

Hyperphagia

Dethier and Bodenstein (1958) cut the recurrent nerve of *P. regina* just anterior to the corpus cardiacum and, by so doing, produced hyperphagic flies. They interpreted this result to mean that cutting the recurrent nerve interrupted the neural pathway to the brain from unidentified receptors in the foregut, the stimulation of which by ingested solutions normally elevates the taste threshold. This interpretation was supported by the observation that flies made hyperphagic on a 1 M sucrose solution responded, after they had disadapted, to a 0.1 M solution. However, some criticisms of these experiments and their interpretation may be made:

(1) No quantitative criterion of hyperphagia was given.

(2) All tests were performed on sucrose solutions. There are no published data regarding the effect of ingestion of this sugar on subsequent taste thresholds.

(3) The method of feeding departed from the usual in that flies were left in contact with the sucrose solution for long periods or were given repeated opportunities to feed. Especially because sucrose is among the most stimulating sugars for the blowfly, the quantities ingested would be expected to be considerably greater than normal.

(4) Dethier and Bodenstein (1958) stated that cutting of the recurrent nerve prevents emptying of the crop. If this is so, any failure of taste threshold to rise could just as well be explained by the absence of sugar in the region of the foregut which contains the threshold-regulating mechanism.

(5) The operation may involve damage to a number of other tissues (muscles, air sacs, and esophagus). In its execution, the corpus cardiacumallatum complex is denervated and handled. Recently, several workers have shown that hormones affect feeding and other aspects of behavior in insects. De Wilde (1958) has shown that the corpus allatum is necessary for feeding in the Colorado potato beetle. Ozbas and Hodgson (1958) found that extracts of the corpus cardiacum reduced the spontaneous activity of the central nervous system and locomotor activity in the roach *Blaberus*. Subsequently, Hodgson and Geldiay (1959) reported that operative shock and other trauma caused release of this material from the gland. Any observed effect of the recurrent nerve sectioning could possibly be due, wholly or in part, to side effects of the operative technique.

Evans and Barton Browne (unpublished) have carried out experiments designed to throw light on some of these points of criticism. The operative technique used was the same as that described by Dethier and Bodenstein (1958), except that the flies were briefly anaesthetized with carbon dioxide during preparation for the operation and testing. (We are indebted to Dr. Bodenstein for instructing us in the method of this difficult operation.)

The recurrent nerves of 48 flies taken from groups of standardized (24 hour starved) flies were sectioned. Others of the groups were given

sham operations which consisted of opening the neck membrane and proceeding with the operation until the corpus allatum-cardiacum complex was visible. Still others were kept as unoperated controls. All the flies were mounted on waxed sticks for testing. One hour or more after the operation and mounting, ascending thresholds to glucose solutions were obtained for all flies. In general these thresholds were greater for the two operated groups than for the controls. Those flies which did not respond to a 0.5 M solution were discarded. Next, all flies were fed once on a 2 M glucose solution until feeding ceased. One hour later glucose thresholds were again obtained. It was found that the thresholds of all three sets of flies at this time were similar. No fly responded to a concentration of less than 1 M and many in each group failed to respond to a 2 M solution. All flies were then fed repeatedly from a brush dipped in 2 M glucose; 15 of the flies which had had their recurrent nerves sectioned became hyperphagic. Only flies found, at the end of the experiment, to have crop weights of 50 mg or more were considered to be hyperphagic. No flies in either the control or sham operated sets were found to have a crop weight above 40 mg. The ascending thresholds of all flies which had sectioned recurrent nerves were repeatedly measured. All had high thresholds, and the hyperphagic ones especially so. None of these responded to 2 M glucose even if allowed both tarsal and labellar contact.

To ascertain that the use of the ascending method of determining thresholds did not give falsely high thresholds, the flies were tested by transferring them directly from water to the 2 M solution without contact with the lower concentrations. Similar results were obtained by this method.

Tarsal thresholds to sugar solutions can only be obtained after the tarsal chemoreceptors have been adapted to water. Hyperphagic flies often were found to have an abnormal response, in that they repeatedly responded to water alone. Because of this it was necessary to retest the response of each fly to water after it had given a positive response to a sugar solution so as to verify that the response was, in fact, to sugar. We feel that the abnormal water response might be involved in explaining the discrepancy between our results and those of Dethier and Bodenstein (1958), in that the persistent hyper-sensitivity to water would tend to mask any elevation of the sugar threshold.

No direct investigation was made of the possibility that damage to some organ other than the recurrent nerve might have been involved in the production of hyperphagia. Both of us did, however, gain an impression that the neatest operations were not the ones that gave rise to hyperphagic flies. Unfortunately, we were unable to devise an appropriate control operation to test this impression. A small-scale experiment was carried out to test the assertion made by Dethier and Bodenstein (1958) that flies with sectioned recurrent nerves are unable to pass sugar from the crop into the foregut and thence through the cardiac valve into the midgut. The recurrent nerves of a number of flies were cut and the flies given repeated opportunities to feed on

2 M glucose. Those which became hyperphagic were allowed to remain mounted on wax sticks. Most of them survived for more than 2 days and even after only one day were no longer bloated. Repeated feeding at any time caused these flies to become hyperphagic again. Since absorption occurs only in the midgut (Evans and Dethier, 1957; Hudson, 1958), it is clear that sugar solution must have passed from the crop into the midgut. Additional evidence for emptying of the crop is that hyperphagic flies were frequently observed to regurgitate.

If cutting the recurrent nerve does in fact lead necessarily to hyperphagia, explanations other than interference with threshold regulation are possible. For instance, although crop distension probably play no part in the control of ingestion when a normal volume is ingested (Evans and Dethier, 1957; Dethier and Bodenstein, 1958), intake, especially the rate and pumping force, might well be influenced by sensory input from the crop when the crop and abdomen are distended by two or three times their normal maximum volume. The force of distension was sufficient on occasion to rupture the abdominal wall.

In view of the evidence available, we conclude that some aspect of the operation did upset the mechanism controlling the intake of food in such a way as to allow hyperphagia to occur. We feel, however, that the mechanism involved has not yet been satisfactorily demonstrated and that threshold regulation probably is not altered by the operation.

Locomotor Activity

Locomotor activity is another aspect of the behavior of *P. regina* which is influenced by feeding and starvation (Barton Browne and Evans, 1960). Flies starved for 24 hours were found to be at least 4 times more active than those fed to repletion on strong sugar solutions. Feeding on the non-utilizable sugar fucose was even more effective in reducing activity than was feeding on glucose. Hence, as is the case with taste threshold, the metabolic state of the tissues is not the determining factor. Blood sugar concentration was also eliminated as a possible determinant by the observation that fucose-fed flies were fully active 27 hours after feeding, at which time their blood sugar concentration was very high. It was found that locomotor activity increased steadily with time after feeding on either glucose, mannose, or fucose, whereas the threshold increased to a peak some hours after feeding when flies were fed either of the latter two sugars (Fig. 1). Hence taste threshold and activity are not well correlated and bear different relationships to one another in flies fed different sugars. This finding is interpreted as evidence that the mechanisms by which the ingestion of sugar controls threshold and locomotor activity are not identical. Locomotor activity seems best correlated with crop volume and hence with the rate of emptying of the crop. Injection of water into the haemocoels of flies greatly reduced their activity. This result suggests that dilution of the blood may have been the ultimate factor determining locomotor activity after feeding.

ECOLOGICAL ASPECTS

Any attempt to apply the available data on the changes in threshold and locomotor activity after feeding to feeding behavior under natural conditions is hampered by the paucity of information about the normal feeding habits of even the major species of blowflies. It seems safe, however, to generalize that most adult blowflies feed on nectar, honeydew, and decaying materials, especially carrion. It is first of interest to know the concentrations of sugar solutions available in nature. Hocking (1953) lists a number of species of plants as having nectar consisting of sugar solutions of a very high concentration, some even exceeding 70 per cent sugar. In most nectars sucrose, glucose, fructose, and less commonly, maltose, are present (Wykes, 1952). Certain nectars would, therefore, be extremely stimulating. Honeydew is known to contain the stimulating sugars fructose, glucose, and sucrose (Gray and Fraenkel, 1954), and whatever its concentration at the time of its production, evaporation would soon increase this. Results given in this paper indicate that the crops of flies that feed on meat can be as full as those of flies that feed on highly stimulating sugar solutions and that meat ingestion raises the sugar threshold to a high level. The situation may be summarized by saying that the flies have access to many sources of food, that many of these are highly stimulating, and that large amounts of them would be ingested if encountered. In nature, therefore, the flies are confronted with a complex "preference-aversion" situation. In this type of situation it has been shown that when flies are given a choice of two acceptable solutions, one of which is more stimulating than the other, almost all feeding is on the more stimulating one (Dethier and Rhoades, 1954). The same result would be expected in nature in places where there is an abundance of food. This is borne out by the observation of Hocking (1953) that many specimens of blood-sucking insects which had been caught in the field had highly concentrated sugar solutions in their crops. Only under conditions where the supply of food was inadequate would ingestion of the less stimulating solutions be expected.

Barton Browne and Evans (1960) have shown that the locomotor activity of *Phormia regina* falls to a low level after the flies have fed to repletion and steadily increases again with starvation, and that the level of activity is a function of the volume of the crop. This means that flies, after a small period of almost complete inactivity immediately after feeding to repletion, begin to move and hence encounter food, and that the frequency of encounters would increase as the flies became more starved. Although the activity of flies which had ingested smaller than normal amounts was not tested, it is highly probable that these do not become as inactive as flies which have fed maximally.

Evans and Dethier (1957) demonstrated that the taste threshold of *P. regina* fed to repletion on any one of a number of sugars, was never so high that a large percentage of the flies failed to respond to the highest concentrations of sugars. For instance, flies fed to repletion on 2 M glucose have a mean threshold to glucose of 1.5 M; hence

more than half of them were able to respond again to 2 M glucose as soon as disadaptation had occurred, even though threshold was maximal. Furthermore, it has been shown above that, at least for flies fed 2 M glucose, feeding duration, and therefore, probably, the volume intake of 2 M glucose, increased with time after feeding, and by 3 hours had become quite appreciable. It is clear from these results that flies are able to make use of encounters with highly stimulating solutions even a short time after feeding to repletion. Other experiments described above indicate that the level to which the threshold rises depends on the volume and the concentration of the sugar ingested. Hence, a fly which is interrupted in its feeding, or which feeds on a solution which is not highly stimulating, would immediately be able to respond to and probably imbibe appreciable quantities of the more stimulating solutions.

It is apparent that control of locomotor activity and food intake, after feeding, work in harmony in *Phormia,* in that the chance of encountering food increases as the fly becomes more and more able to take in more food. These mechanisms, working together, would tend to keep the flies in nature continuously more or less fully fed in areas where food materials are abundant.

The role of odor is difficult to assess. Apparently nutritional state as a variable in studies of attractants and repellents has not received much attention. One might expect that fed animals would be less responsive to attractants than starved, and such a result has been reported for mosquitoes (Christophers, 1947).

However, the primary effect of feeding might be on locomotor activity, rather than responsiveness to the odor *per se*. Odor certainly attracts flies to decaying materials, but data reported above suggest that the odor has no affect on the intake of liver by blowflies. Some species of blowflies are reported to feed on flowers with fetid or carrion-like odors (Hall, 1947). In these cases, it is not known whether the odor acts only as an attractant or whether it also acts as a feeding stimulant. In this latter case, one must distinguish between odors which evoke extension of the proboscis and those which augment intake of a test solution, since some that cause extension by the blowfly greatly diminish intake of sugar solutions (Evans, in preparation).

HUNGER

In a study such as the preceding, it does not appear possible to employ the word "hunger" in a meaningful and useful sense. The term implies a unitary phenomenon; consequently it should refer to a single process which is causally linked to all the overt manifestations of feeding and starvation. Use of the term before there is experimental evidence that such a common path exists is an assumption, conceivably a misleading one. In the present case, the three aspects of behavior that have been studied appear instead to be independent functions. The blowfly may under different conditions be hungry with respect to nutrition, locomotion, or readiness to feed, each independently of

the others. A possible compromise would be to restrict the term to one aspect of the total behavior, most likely to readiness to feed. But this usage becomes repugnant when the animals die of starvation although they will not feed and therefore are not "hungry."

In view of these considerations, the word "hunger" in such cases is at best inutile and is perhaps even prejudicial, except possibly after the fact when the several manifestations have been shown to have a common causation.

Summary

Starvation has several behavioral manifestations in the blowfly. At present, taste sensitivity to carbohydrates, food intake, and locomotor activity are recognized, all of which increase during starvation. The mechanisms whereby ingestion accomplishes these changes have been analyzed in physiological terms.

Much evidence indicates that it is the presence or absence of solutions in the foregut, exclusive of the crop, that regulates taste sensitivity to carbohydrates, but the report that transection of the recurrent nerve interferes with threshold regulation could not be confirmed. It is pointed out that a hormonal link in the pathway of threshold regulation has not yet been excluded as a possibility and that such a hypothesis would account for the typical delay of threshold elevation after ingestion.

From the knowledge of the behavioral taste threshold, other aspects of the ingestive act are predictable. An adequate and acceptable stimulus to chemosensory hairs is sufficient to evoke proboscis extension (by definition), spreading of the labellar lobes, and initiation of sucking, all of which continue until adaptation has proceeded to a level that renders the solution effectively tasteless. The "sweetness" of the solution determines the rate of ingestion, as well as affecting adaptation time. After ingestion, the time-course of disadaptation and of threshold elevation determine taste threshold. Thus, the initiation, maintenance, termination, rate, and duration of ingestion are regarded at present as relatively simple neurophysiological functions.

Feeding and starvation apparently act via a different mechanism to affect locomotor activity. If the term "hunger" is employed, one must say that the blowfly may be hungry with respect to nutritional state, to taste threshold or readiness to ingest, and to locomotor activity, each of which is experimentally dissociable from the others.

Some ecological implications of these findings are discussed. A new method of obtaining behavioral taste thresholds is described which gives statistically satisfactory results when as few as twelve flies are employed.

Addendum

We and all the earlier references on this subject have apparently been unaware of the pertinent evidence of M. Day (1943. *Biol. Bull.*, 84:127-140) on *Lucilia* and *Sarcophaga* and E. Thomsen (1952. *J. exp. Biol.*, 29:137-172)on *Calliphora.* Both noted in asides to their main points that certain operations on endocrine systems associated with the stomatogastric nervous system

produced bloated flies. Both recognized that the bloating was a consequence of excessive water ingestion and that it developed in only a fraction of the operated flies. Thomsen confirmed Day's observation that removal of the ring gland from flies just after eclosion had this effect. Thomsen obtained similar results upon extirpation of the medial neurosecretory cells of the brain which join the recurrent nerve and end in the endocrine organs of the ring gland. Day also cut the recurrent nerve, apparently without noticing such an effect. While the hyperphagia is not explicable at the present time, these results and our discussion point up several common features: hyperphagia is not an invariable concommitant of any of the several surgical procedures; imbibition of water is responsible for the bloating, at least in part; and the hyperphagia is as closely associated with endocrine systems as with purely nervous pathways.

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Vegetation Zonation on the Shore of a Small Lake[1]

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The occurrence of more or less well-marked, concentric zones of vegetation parallel to the margins of lakes has been frequently noted and described as zonation (Dansereau 1945, Raup 1935). It is commonly ascribed to the existence of continuous bands of different habitats which parallel the shore line. The distinctiveness of the zones is due to the different physiognomies of the vegetation and presumably the zones are differentiated by their species composition. The zones described may be very wide or, in some cases, narrow bands parallel to the shore. They may be continuous or interrupted by areas of different vegetation, if the environment varies abruptly across the pattern of the zones, resulting in an alternation of different vegetational communities which occupy the same position relative to the shore line (Braun-Blaunquet, 1932). The present work was designed to study quantitatively the composition of zones of vegetation paralleling the shore of a small lake.

Description of the Area

Duck Lake is a small, dystrophic lake located about one mile northeast of the Kellogg-Gull Lake Biological Station of Michigan State University. (T1S., R9W., Sec. 5, SE ¼) Kalamazoo County, Michigan. It is almost round, quite shallow, and has no outlet or inlet. Much of the shore line has a luxurious zone of *Nuphar advena* which extends well into the body of the lake. The water is alkaline with a pH of 8.0 at the time of the study in July and August of 1959. The water level is controlled by the level of the water table and has fallen during the past ten years exposing a slightly sloping surface (1.5%-2.0%). This study is restricted to the narrow band (7-12 m), on the south shore of the lake, extending from the present water line to a distinct line of shrubs which marks the higher water level. This is comparable to the grève or strand of Dansereau (1945). Local residents said that the line of shrubs marked the shore of the lake ten years ago and it had been at that level for as far back as they could remember. Iron posts for tying up boats and abrupt terminations of paths indicate that this was in fact the old shore line. The study area had been submerged until approximately ten years ago and has been exposed as the water receded. Two distinct bottom

[1] Contribution No. 111 from the Kellogg Gull Lake Biological Station, Hickory Corners, Michigan.

types were exposed: sandy areas now only sparsely covered by emergent vegetation; and muck areas which are densely covered at present.

METHODS

Transects were established at right angles to a tangent on the lake shore. Three were placed in the sandy area and two in the muck bottom area. They extended from the present shore line to the older shore line, a distance of seven meters on the sand and twelve meters on the muck. Each transect was one decimeter wide. Each meter of a transect was divided into ten square decimeter quadrats. Species occurrence in each of these was recorded. Density counts of each species were made in the fifth and tenth quadrats of each meter. Nomenclature follows Gleason (1952).

RESULTS

The apparent zonation of the vegetation on the recently exposed shore line of the lake is due to the larger size of the plants in areas

TABLE I.—Average frequency per cent in transects on muck bottom

Species	Meter											
	1	2	3	4	5	6	7	8	9	10	11	12
Nuphar advena	20	20	20	15		10	10	30	10			
Potamogeton natans				5								10
Hemicarpha micrantha	95	100	65	50	20	5						
Hydrocotyle umbellata	80	75	70	80	90	30	10	5				5
Carex sp.	15	15	10		10	20	10					
Peltandra virginica		5	5									
Juncus coriaceus			30	15	35	15	5					
Polygonum punctatum			15			5	10	10	10	10		
Gramineae sp.			40	40	20	30	15	20	10			15
Gerardia purpurea					35	30	25	30	25			
Salix sp.				20	10	10						
Cyperus strigosus					20	10		15				
Juncus effusus				30	10	10	50	30	25	10	20	
Juncus tenuis						10	10	20				
Lycopus americanus			10	30	30	40	40	20	20	20	45	25
Solidago sp.					25	30	35	35	60		45	35
Impatiens pallida							15	5	15	25		
Eupatorium perfoliatum				10	10	40	35	40	35	55	70	70
Spiraea alba					5							
Carex crus-corvi							10		5	10	25	
Juncus militaris					5				5			
Lactuca canadensis					5			10	15			
Verbena hastata								10			5	
Potentilla anserina										5	5	
Hypericum boreale										5		
Hieracium sp.										10		
Cephalanthus occidentalis											5	15
Aster sp.								10		5		10
Cirsium arvense										15	5	15

TABLE II.—Average frequency per cent in transects on sandy bottom

Species	Meter						
	1	2	3	4	5	6	7
Nuphar advena	3	10	3				
Potamogeton natans	10	7	3				
Hemicarpha micrantha	33	83	87	97	53	43	27
Hydrocotyle umbellata	23	60	73	47	20	53	37
Juncus sp.	10	10	33	13	33		13
Juncus coriaceus		3	50	57	20	17	7
Polygonum punctatum			3	3			
Gramineae sp.		3	13	33	27	13	20
Carex sp.			3	13	27	10	3
Gerardia purpurea			3	40	60	100	80
Salix sp.			3	30	30	17	17
Rorippa palustris			7				
Eleocharis palustris			7	7			
Dulichium arundinaceum				10	7		
Lycopus americanus			7	10	30		3
Carex cryptolepis					13	3	
Impatiens pallida					10	3	10
Eupatorium perfoliatum						3	17
Spiraea alba					10	10	7
Quercus sp.						3	
Juncus tenuis				3		3	
Lycopus uniflorus							13
Fabaceae sp.				7	13		

TABLE III.—Average density on muck bottom of the more common species

Species	Meter											
	1	2	3	4	5	6	7	8	9	10	11	12
Hemicarpha micrantha	78.0	80.0	18.0	10.0	2.5							
Hydrocotyle umbellata	4.0	5.7	9.0	8.7	1.0							
Juncus coriaceus			1.2	1.2	3.7	0.7	0.2					
Gerardia purpurea					1.0	1.0	0.2	1.5	0.5			
Juncus effusus				1.0		0.7	2.5	2.2	1.0		0.5	
Lycopus americanus				1.2	0.2	1.0	0.5		0.5	0.7	0.5	0.2
Solidago sp.					0.2	1.0	1.5	1.2	0.7		1.5	
Eupatorium perfoliatum				0.2	0.2	1.0	1.5	0.5	0.2	1.5	1.7	2.2
Average density of all species.	82.2	86.1	30.2	24.3	9.7	7.5	7.3	6.4	5.0	4.0	5.7	3.2

TABLE IV.—Average density on sandy bottom of the more common species

Species	Meter						
	1	2	3	4	5	6	7
Hemicarpha micrantha	4.8	10.8	11.7	10.3	4.0	3.3	1.0
Hydrocotyle umbellata	1.5	25.7	7.8	1.5	1.0	1.5	0.2
Juncus sp.		0.5	2.7	0.7	0.5	0.8	
Juncus coriaceus		0.3	1.0	2.3	0.5	0.5	
Gerardia purpurea			0.7	2.0	3.2	8.8	6.8
Lycopus americanus					0.3	0.3	0.2
Eupatorium perfoliatum						0.2	0.3
Average density of all species.	6.8	38.2	25.0	19.8	11.0	17.4	9.9

more distant from the water's edge. The first few meters on both sand and muck bottoms are dominated by two small species, *Hemicarpha micrantha* and *Hydrocotyle umbellata* (Tables I-IV). These two constitute over seventy-five per cent of the average density in each of the first three meters on the sand bottom and in the first four meters on the muck although the average density of *Hemicarpha* is much lower on the sand. Beginning with the third and fourth

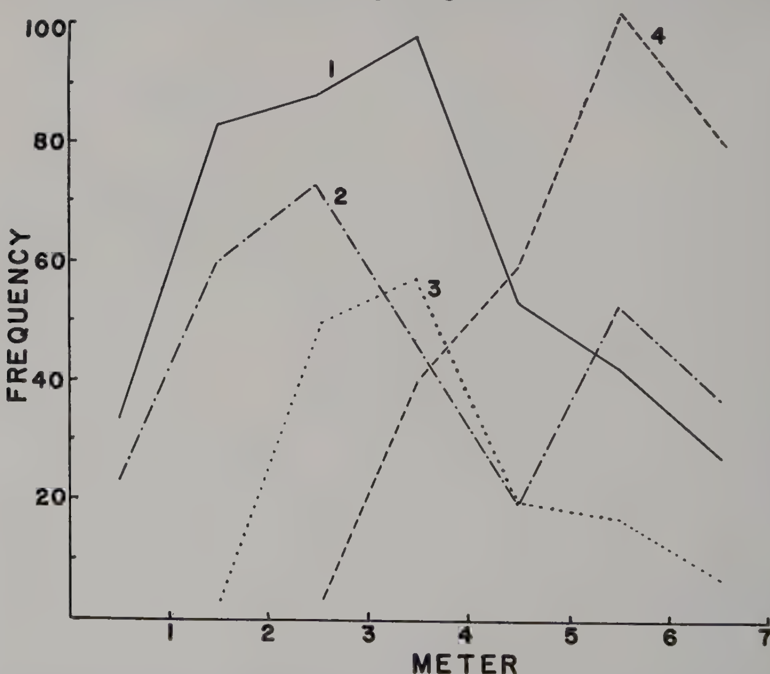

Fig. 1.—Average frequency per cent in each meter of common species on sand bottom. 1. *Hemicarpha micrantha*, 2. *Hydrocotyle umbellata*, 3. *Juncus coriaceus*, 4. *Gerardia purpurea*.

meters larger plants appear which, because of their size, if not their numbers, give the impression of a distinct zonation.

The composition of the vegetation, however, does not exhibit a sharp change at any point along the transect. Rather there is a gradual transition in the composition of successive meters. This is evidenced by the changes in frequency per cent of some of the common species (Figs. 1 and 2). Similar changes are exhibited if average density is used instead of frequency.

It is not surprising to note that the average density, especially in the muck transects, diminishes in the segments of the transect farther from the shore line (Table III). This is due simply to the larger size of the individual plants relative to the sample size (1 dm^2). The first two meters of both sand and muck bottoms are very similar in composition, *Hemicarpha* and *Hydrocotyle* comprising over ninety per cent of the relative density in both cases. Beyond the second meter the proportion of these two species drops off and does so more rapidly in the muck transects than in the sand transects. This is also true of the average density and average frequency.

The change in composition is also illustrated by comparing each meter with the others by means of the "Index of Similarity" (Bray

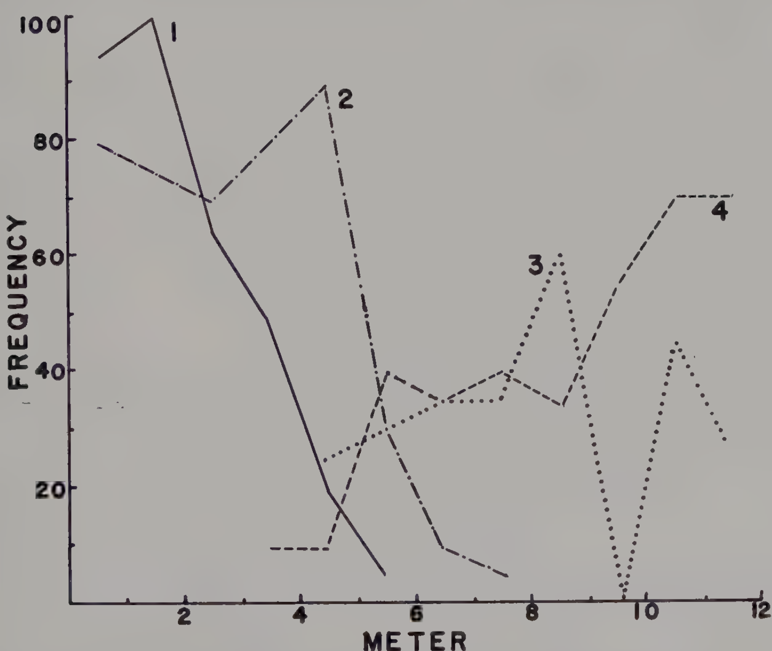

Fig. 2.—Average frequency per cent in each meter of common species on muck bottom. 1. *Hemicarpha micrantha,* 2. *Hydrocotyle umbellata,* 3. *Solidago* sp., 4. *Eupatorium perfoliatum.*

TABLE V.—Matrix of Index of Similarity values based on relative density for successive meters on sand bottom

	Meter 1	2	3	4	5	6	7
1.		51.7	68.9	58.7	35.5	27.5	11.7
2.			62.8	38.4	40.0	29.7	11.7
3.				65.7	58.0	38.5	15.0
4.					66.6	43.4	25.0
5.						68.4	49.7
6.							77.6

and Curtis, 1957). This index is derived by summing the lower values of any relative measure of composition, e. g., per cent density, for those species which are common to the two samples being compared. If they have identical values for the same species the index would be 100. If no species are common to the two samples the index would be 0. The matrix of index values based on per cent density in the sand transects exhibits a gradual progression of values (Table V). Each meter is, in general, most like its nearest neighbors in the transect and least like those most distant. In the transects on the muck bottom the same gradual sequence of compositional changes is evidenced in the first seven meters but beyond the seventh meter the values are rather erratic and proximate meters may be quite different in composition as indicated by low index values (Table VI).

The first two meters on both sand and muck substrates are very similar in composition of the vegetation. In the third meter of the sand transects *Gerardia purpurea* appears and it becomes increasingly important in subsequent meters, being the leading dominant in the sixth and seventh meters. *Gerardia* also appears in the fifth meter of the muck transects but does not continue as a prominent component in subsequent meters. In this case taller species, *Solidago* sp. and *Eupatorium perfoliatum,* especially the latter, become the most important components.

TABLE VI.—Matrix of Index of Similarity values based on relative density for successive meters on muck bottom

	Meter 2	3	4	5	6	7	8	9	10	11	12
1.	97.9	64.8	45.1	29.8	0.0	0.3	0.0	0.0	0.0	0.0	0.0
2.		66.6	46.9	31.6	0.0	0.3	0.0	0.0	0.0	0.0	0.0
3.			79.1	45.7	10.5	3.3	6.6	0.0	0.0	0.0	0.0
4.				48.5	21.0	9.3	10.0	11.0	7.0	9.0	6.0
5.					33.5	14.1	22.5	17.0	5.0	7.5	5.0
6.						48.9	52.7	46.4	26.0	43.4	20.1
7.							63.0	50.8	32.6	63.7	26.7
8.								47.5	7.7	35.5	7.7
9.									14.3	35.4	11.9
10.										39.1	42.4
11.											44.6

DISCUSSION

The exposure of two very different types of substrate, sand and muck, as a result of the lowered water level of the lake affords an opportunity to examine and compare the composition and distribution of the vegetation occupying the newly exposed areas. The first four meters in either case are dominated by the same species, *Hydrocotyle umbellata* and *Hemicarpha micrantha.* The water level and perhaps physical or chemical characteristics of the water are apparently the primary factors influencing the vegetation in these segments of the transects. This is suggested by the gradual diminution in the importance of the two major dominants in each successive meter away from the water's edge. In some species, especially *Gerardia purpurea,* the individual plants nearest the water's edge were small and spindly and increased in size away from the water's edge.

Beyond the fourth meter the vegetation on sand and muck become increasingly dissimilar so that by the last comparable meter, the seventh, there is little or no similarity between the vegetation on the two substrates. Here the difference in the substrate, especially the ability of the muck to hold and supply water more effectively than the sand, becomes of primary importance. This is made evident by the persistence of hydrophytes such as *Nuphar advena* and *Potamogeton natans* much farther from the water's edge on the muck than on sand. *Nuphar* persists as large although prostrate plants to the ninth meter on the muck bottom, whereas, on the sand it persists only to the third meter as depauperate specimens.

The vagaries of the Index of Similarity values in the transect segments beyond the fourth meter on the muck are due to the increasing heterogeneity of the vegetation. Once distance from the water's edge is no longer the primary factor influencing the vegetation the proximate segments in the transect are no longer particularly similar.

There is no record of water level at Duck Lake to show whether the drop in water level was continuous or marked by irregular fluctuations. Records of the W. K. Kellogg Bird Sanctuary of Michigan State University, located less than one mile away on Wintergreen Lake, indicate that levels at Wintergreen Lake have dropped, reaching low levels in 1958 and 1959. If it reacts similarly to Duck Lake, which seems probable as both lakes are runoff and spring fed, the drop was not continuous. Water levels show an annual cycle of fluctuation and though the general trend since 1949 has been down, an abrupt drop in 1953 is followed by a slight rise in 1954-1955 and a gradual, continuous drop to 1959. The past three years, according to Dr. R. D. Van Deusen, the Director, have been years of low water.

A study of shore line plant succession controlled by irregular fluctuations of the lake level by Graham and Henry (1933) describes the resulting vegetation as forming discrete zones as seral units. Galiano (1957) also describes well defined associations (*sensu* Braun-Blanquet) related to annual changes in water level.

The results of the present study indicate a gradual change in composition along the transects. The apparent zonation close to the shore line is due to a physiognomic distinction rather than a compositional one. The specific composition of the vegetation and the changes noted are not necessarily typical of lakes in this region. At least little comparative data of a quantitative nature is available. In this instance the apparent zones are not divisible into well-defined communities or zonal bands by any but arbitrary criteria.

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Structure and Functions of the Thyroid Gland in Reptiles[1]

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Reference to recent general reviews concerning thyroid morphology and physiology reveals a paucity of information for Reptilia as compared with any other vertebrate class (Eggert, 1938; Goldsmith, 1949; Fleischmann, 1951; Lynn and Wachowski, 1951; Gorbman, 1955; Kollros, 1959). This paper gives an account of the present state of knowledge of the reptilian thyroid in the hope of stimulating further researches in this field.

Historical

Although several early anatomists noted the thyroid gland in a few reptiles, Simon (1844) seems to have been the first to clearly distinguish thyroid from thymus in lower vertebrates and to attempt a comparative account of its morphology. Leydig (1853) made an early study of both gross and finer structure of the thyroids of *Testudo graeca* and *Coluber natrix*. The first embryological investigation of the gland in a reptile is that of de Meuron (1886) for *Lacerta agilis*. Experimental approach to study of the functions of the reptilian thyroid began with the work of Christiani (1894a,b, 1895a,b,c, 1900, 1903) who devised methods for thyroidectomy and thyroid transplantation in lizards, snakes, and turtles.

Gross Morphology

In turtles and in snakes the thyroid is an unpaired gland, spherical, ellipsoidal, or ovoid in shape, just anterior to the heart. In Crocodilia it consists of two well-defined lobes lying on either side of the trachea with a narrow connecting isthmus. In *Sphenodon* it is a single, narrow body, transversely elongate. Lizards show a wide variety of thyroid forms with unpaired, bilobed, and completely paired glands found even in different members of the same family.

Detailed descriptions of the anatomical relations of the thyroid are available for a number of lizards and for *Sphenodon*. For other reptiles published information is scanty.

Study of the lizard thyroid begins with the work of Simon (1844) who pointed out the wide diversity of thyroid form in the Lacertilia as exemplified in representatives of the families Lacertidae, Iguanidae, Gekkonidae, Chameleontidae, Scincidae, and Amphisbaenidae. The

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bilobed thyroid of *Uromastix* was described by Calori (1862) and that of *Phyllodactylus* by Wiedersheim (1876). Van Bemmelen (1887) gave a brief account of the vascular supply to the gland in *Platydactylus, Anguis,* and *Lacerta* chiefly emphasizing the presence of two pairs of thyroid arteries. Thyroid morphology in several African lizards was discussed by Viguier (1909a,b, 1911a). The arterial supply was given for *Uromastix* by Bhatia (1929) and for *Hemidactylus* by Bhatia and Dayal (1933). Bourne (1935) considered the thyroid of *Egernia kingii* as unique in being a narrow, ribbon-like structure lying transversely across the trachea but this condition is found in a number of other lizards (Lynn and Walsh, 1957).

The most complete account of the anatomical relations of the thyroid in a lizard is that of Adams (1939) for *Lacerta.* In this animal the gland lies dorsal to the muscles constrictor colli, episternohyoideus superficialis and profundus as a broad structure widest at the center and tapering at the ends. It is ventral to the trachea and just anterior to the divergence of the carotid arches. The arterial supply is by a pair of superior thyroid arteries arising from the external carotids and a pair of inferior thyroids from the laryngeo-tracheal branch of the pulmonary artery. Paired thyroid veins enter the vena trachealis (external jugular of Bourne) which, in *Lacerta,* is present on the right side only. Innervation is from the inferior laryngeal nerves. Miller (1955) described a quite similar vascular supply in *Xantusia.*

A recent survey of thyroid morphology in representatives of 23 families of lizards (Lynn and Walsh, 1957; Lynn and Komorowski, 1957) emphasizes the multiplicity of forms assumed by the gland in this group and the wide divergence from the usual condition which may be found in certain specialized families like the Amphisbaenidae where the thyroid may be extremely long and attenuated and situated far anterior to the heart.

The lizard thyroid is usually contained in a large lymphatic space and is often also enveloped in adipose tissue (Pischinger, 1937). In *Gymnodactylus* the gland is reported to be fused with a thymus-like tissue complex (Eggert, 1934b).

Although the turtle is widely used as a laboratory animal the only full account of thyroid morphology is that of Naccarati (1922) for *Emys europaea* and *Testudo graeca.* In these the gland is spheroidal, located a little to the right of the midline in the cavity of the arch of the innominate trunk. Volume and weight of the thyroid show a high degree of individual variation. In *Emys* it lies at the level of the divergence of the bronchi, in *Testudo* it is posterior to this level. Paired superior and inferior thyroid arteries arise from innominate trunks and carotid arteries respectively. The paired thyroid veins unite with the accessory pectoral veins and enter the subclavians. A rich lymphatic drainage is present. Innervation is from the cervical sympathetics and the laryngeal branches of the vagi.

Published accounts of ophidian thyroid morphology are limited

to brief descriptions for two subspecies of the water-snake, *Natrix sipedon* (Thompson, 1910; Bragdon, 1953) and some incidental observations on *Zamenis* and *Coleopeltis* (Francescon, 1929).

No paper dealing with the gross anatomy of the crocodilian thyroid has come to hand.

Sphenodon, the sole living representative of the Rhynchocephalia, has naturally attracted special interest. Its thyroid was described by van Bemmelen (1887) who noted the presence of two pairs of thyroid arteries just as in lizards. O'Donoghue (1920), in a detailed study of the vascular system described the superior thyroid arteries as branches of the external carotids and the inferior thyroids as branches from the pulmonary arch. The thyroid veins enter the precaval by way of the brachials. Adams (1939) noted that the anatomical relations of the thyroid in *Sphenodon* are similar to those in *Lacerta*.

Gross pathological enlargement of the reptilian thyroid seems rare. Only two cases have come to notice. Pick and Poll (1903) described a large adenomatous goiter in a pleurodiran turtle (*Platemys*) and Muller (1926) recorded a parenchymatous and cystic colloid goiter in the lizard *Zonurus*. Both these animals had been kept in captivity for some years.

EMBRYOLOGY

The origin and early development of the reptilian thyroid shows no unusual features. The anlage of the gland arises as an evagination of the pharyngeal floor at the level of the first pair of pouches. Paired lateral anlagen do not seem to be involved in any reptile. After separation from the pharynx the cells of the thyroid rudiment become arranged into cords or clumps. As posterior migration occurs the gland becomes encapsulated and the cell cords break up into organized follicles. Various aspects of these phases of development have been described for lizards (*Lacerta*: de Meuron, 1886; Maurer, 1898, 1899; Peter, 1901; Eggert 1934a; *Anguis*: Prenant, 1896; *Tarentola*: Viguier, 1909a; *Seps*: Dorello, 1909a, b; *Sphaerodactylus*: Walker, 1951; Cheverie, 1959), turtles (*Chelonia*: van Bemmelen, 1893; *Chrysemys*: von Alten, 1914; Shaner, 1921; *Chelydra*: Dimond, 1952), crocodilians (*Alligator*: Reese, 1910; Hammar, 1937; *Crocodilus* and *Kaiman*: Hammar, 1937) and one snake (*Thamnophis*: Harrison and Denning, 1929). The embryology of the thyroid of *Sphenodon* has not been described.

The time of appearance of organized follicles and of colloid within the follicles is of interest since these features may be taken as indications of the onset of secretory activity. Only a few of the papers cited give precise information on these points. Maurer (1899) found organized follicles beginning to form in embryos of *Lacerta agilis* 21 days after the eggs were laid but colloid was first seen at 31 days (the next stage studied). Eggert's (1934a) much more detailed study for this species and for *L. vivipara* revealed somewhat earlier appearance of these features: follicles well defined at 20 days

(Peter's Stage 32); intrafollicular colloid at Stage 33. Recent work of Cheverie (1959) on *Sphaerodactylus* agrees closely with Eggert's findings. In the turtle, *Chelydra*, (Dimond, 1952) follicles first appear in the 20-day embryo but stainable colloid is not present until the 23rd day.

HISTOLOGY AND CYTOLOGY

Detailed histological consideration of the reptilian thyroid began with Galeotti's (1896) account of the changes in the follicular epithelium in turtles treated with certain toxins. Later Viguier (1909a, b, 1911a) gave brief descriptions of normal thyroid histology in several lizards and Naccarati (1922) provided rather full accounts for *Emys* and *Testudo*. Barchiesi (1928) discussed the effects of prolonged starvation upon the turtle thyroid and pointed out, what is now well recognized, the enormous variability in thyroid histology in normal turtles. Bussi (1929) described the reticular network around the thyroid follicles in several repti[illegible]s in birds and amphibians. The general histology of th[illegible]ake thyroid has been described by Hellbaum (1936).

Beginning with the work of Weigmann (1932) there has been considerable interest in seasonal changes in the activity of the reptilian thyroid and this has resulted in the publication of several important histological studies. Weigmann found significant seasonal changes in epithelial height in the thyroid of *Lacerta vivipara* which indicated a much greater functional activity in summer than in winter. Eggert (1935a) carried out a detailed study over a period of several successive seasons for three different species of *Lacerta* and for animals of various ages. He found that the thyroid exhibits signs of maximal activity during June and July. At this time all follicles contain thin, freshly formed colloid with many peripheral chromophobe droplets. The epithelium is high and many cells exhibit mitotic figures. Epithelial height and mitotic rate gradually decrease during late August and September and there is an increase in stored colloid. The gland is most inactive during the winter months when the lizards are in deep hibernation. In young specimens activity begins anew in February and the thick stored colloid is gradually released and replaced by thin newly produced secretion. By April the gland is rather active with only a few peripheral follicles still containing stored colloid. Experiments on the effects of high and low temperature led to the conclusion that the seasonal changes are largely dependent upon environmental temperature (Eggert, 1935b). In addition to the seasonal changes the thyroid also shows brief periods of decreased activity in relation to the growth of the horny layer of the skin preceding ecdysis. Once shedding has occurred the thyroid returns to its normal appearance within 48 to 72 hours. Eggert found no evidence of changes in histology correlated with the breeding season in *Lacerta*.

Wilhoft's (1958) findings for *Sceloporus occidentalis* are in agreement with those of Eggert. Height of the thyroid epithelium is low-

est during the winter (December to February) and highest in summer (June and July). The epithelial height increases gradually during the mating period (April to June). In females the histological appearance of the thyroid indicates a rapid decrease in activity shortly after egg laying. In males there is a more gradual decrease beginning somewhat later. Juveniles show an increase in activity in the spring which reaches a maximum during June and July. Wilhoft also demonstrated that prolonged exposure to temperatures which are optimal for normal activity (34 - 35°C) causes death in some animals, a greater frequency of molting in some, and a rise in heart rate and in thyroid epithelial height in all.

In non-hibernating lizards (*Anolis carolinensis* from Louisiana) thyroid histology indicates high secretory activity even during the coldest months and the lowest epithelial heights are found during spring and early summer (Evans and Hegre, 1938). In this species an increase in epithelial height occurs in females during ovulation. The viviparous lizard *Xantusia vigilis,* another non-hibernating form, also shows indication of high secretory activity in the winter, December through March, but a further increase in activity during April, May and early June when gametogenesis and mating occur (Miller, 1955). In females the thyroid continues to present an appearance of high activity during early gestation but becomes relatively inactive before parturition. The epithelial height reaches its lowest level during late fall (August to December).

Study of the thyroids of turtles (*Chrysemys*) from Montana showed a mid-winter period of inactivity comparable to that found in hibernating lizards (Evans and Hegre, 1940).

Eggert (1935a) also reported age changes in the histology of the lizard thyroid. These are primarily associated with a gradual invasion of the gland by lymphocytes which may form nodules or may spread diffusely through the tissue. Isolated follicles may undergo involution and the spaces resulting from their degeneration are then filled in with fat. Desquamation of the follicular epithelium was also observed in a few specimens. This was not correlated with any particular physiological state or with any phase of colloid release. The shed epithelial cells gradually degenerate and are taken up by lymphocytes.

Iodine Content of the Thyroid

The chemistry of the thyroid secretion is similar in all vertebrates studied. In snakes and fresh-water turtles the iodine content of the thyroid in relation to total body weight is quite comparable to that in other vertebrates (Nosaka, 1926) but the thyroxin content of the gland in sea turtles and alligators is reported to be exceptionally high (Baumann, Metzger and Marine, 1942). Feeding of dried thyroid material from lizards, alligators, or turtles is highly effective in inducing precocious metamorphosis of tadpoles (Drzewicki, 1931, Baumann *et al.,* 1942) and turtle and alligator thyroid effectively raises the basal metabolic rate in rabbits (Swingle and Martin, 1926).

Uptake of radioiodine by the turtle thyroid is subject to great seasonal and individual variation but is within the limits of that found for other animals (Bileau, 1956).

THYROID-PITUITARY RELATIONS

EFFECTS OF THYROIDECTOMY, HYPOPHYSECTOMY OR TSH ADMINISTRATION

It was pointed out quite early (Viguier, 1911c) that the pituitary glands of thyroidectomized lizards (*Uromastix*) increases in size and show vacuolization of the basophil cells. Viguier suggested that the hyperactivity of the pituitary partially compensates for the lack of thyroid secretion. Despite the great interest in thyroid-pituitary relations in vertebrates since that time, only one other paper dealing with the effects of thyroidectomy upon pituitary histology in a reptile has appeared. Siler (1936) found an increase in the number and size of vacuoles in the basophils of the pars anterior of the pituitary after thyroidectomy in the garter snake (*Thamnophis*). There was also an increase in the number of basophils by enlargement and granulation of some chromophobes. The vacuolated basophils ultimately underwent degeneration so that the final result was an actual reduction in pituitary basophils.

Combescot (1955) described characteristic changes in basophils in the turtle (*Emys*) correlated with stages of the reproductive cycle and related these to concomitant changes in thyroid histology. Seasonal changes in pituitary cytology occur also in the garter snake (Hartmann, 1944).

More direct evidence of pituitary control of thyroid function may be derived from studies of the effects of hypophysectomy or of the administration of pituitary extracts. Eggert (1935b) demonstrated the effectiveness of thyrotrophic hormone (TSH) in stimulating thyroid activity in *Lacerta*. Although there is great individual variation in the degree of response, animals given TSH during the summer show a marked increase in the height of the thyroid epithelium, rapid discharge of intrafollicular colloid, and appearance of many intracellular colloid droplets. There is also an increase in mitotic rate which leads to formation of a multi-layered epithelium and ultimately to desquamation of epithelial cells. In hibernating animals however, activation of the thyroid by TSH was not demonstrable. Administration of thyroxin to summer specimens results in rapid reduction in thyroid activity but winter specimens show no response to the treatment. As Eggert points out, this agrees with the hypothesis that a high level of thyroid secretion in the blood serves to depress the pituitary's TSH production. The lizard *Sceloporus* was used by Gorbman (1946) as a test animal for detecting qualitative variations in activity of thyrotrophic hormone preparations, and Mason (1938) suggested the use of the snake *Tropidonotus* for the same purpose.

In snakes (*Thamnophis*) hypophysectomy causes a progressive decrease in the height of the thyroid epithelium which may be cor-

rected by hypophyseal implants (Schaefer, 1933) or by pituitary extract injections (Hellbaum, 1936).

In turtles (*Chrysemys*) a series of 36 daily injections of whole gland pituitary extract causes an increase in height of the thyroid epithelium and a decrease in follicle size which persists as long as 136 days after the first injection (Evans and Hegre, 1940).

EFFECTS OF GOITROGENIC DRUGS

Drugs which interfere with production of the thyroid hormone may be used as a means of effecting "chemical thyroidectomy" and thus furnish an additional method for study of the pituitary response to thyroid deficiency. The earliest use of this technique in reptiles seems to have been by Greenberg (1948) who reported increase in epithelial height and discharge of colloid in the thyroids of young turtles (*Pseudemys*) treated with thiourea. Similar responses were obtained by Pastore (1950) in adult *Clemmys* and *Graptemys* and by Adams and Craig (1950b) in *Chrysemys.* In both these latter studies a great individual variability in degree of responsiveness was noted. Dimond (1954) investigated the effects of thiourea on the embryonic thyroid in *Chelydra* and found that hypertrophy, hyperemia, and colloid discharge is produced in the thyroids of all treated embryos whether the drug is administered early or late in the incubation period.

Lizards of the genus *Anolis* show marked thyroid response to antithyroid agents (Adams and Craig, 1949, 1951; Ratzersdorfer, Gordon, and Charipper, 1949) but *Lacerta* is reported to be almost completely unreactive (Adams and Craig 1950a). In *Anolis* injections of 1.0 per cent thiourea are most effective (Ratzersdorfer *et al.,* 1949) and higher concentrations (2.0%) have toxic effects that partially mask the goitrogenic reaction.

The accepted interpretation of the action of goitrogenic drugs is that they interfere with synthesis of thyroid hormone. The resulting decline in the blood level of thyroid hormone stimulates the pituitary to increase its output of TSH and this is responsible for the histological changes in the thyroid itself. The fact that these drugs do indeed affect hormone production by the thyroid has been demonstrated for many vertebrates by measurement of the thyroid's ability to concentrate radioiodine. Only one such investigation has been made for a reptile. This is the study of Bileau (1956) for *Chrysemys.* Her results confirm previous reports of great variability and relatively low sensitivity of response of the turtle thyroid to goitrogens.

THYROID RELATIONS WITH OTHER ENDOCRINE ORGANS

Several early workers reported that thyroidectomy in lizards causes definite changes in other endocrine organs of the pharyngeal region. Viguier (1911b) described cytological changes in the parathyroids of *Uromastix* after thyroid removal and Drzewicki (1927) found similar effects in *Lacerta.* Drzewicki (1929) and Sembrat and Drzewicki (1936) reported cystic changes in the thymus and hyper-

trophy of the ultimobranchial (postbranchial) bodies of thyroidectomized lizards. The effects on the ultimobranchial bodies were further studied by Eggert (1936b, 1937, 1938b) who ascribed them to direct action of the increased TSH production following thyroid extirpation. He found that the changes can be produced in intact animals by TSH administration alone.

Relations between thyroid activity and gonadal function seem to be well established for some lizards. Mellish and Meyer (1937) found that mature females of *Phrynosoma* show marked atrophy of the ovaries after thyroxin injection. Moreover the thyroids of lizards (*Anolis*) injected with theelin have smaller follicles and higher epithelial cells than do those of controls (Evans and Hegre, 1938). Epithelial height is also increased during normal ovulation. Similar findings have been reported for the Japanese lizard *Takydromus* (Hatta, 1944). The most recent and most complete studies concerning the relation between gonadal activity and the thyroid-pituitary complex are those of Miller (1948, 1955) for *Xantusia*.

THE THYROID IN GROWTH AND DIFFERENTIATION

There is little convincing evidence as to whether the thyroid influences growth rate in reptiles. Drzewicki (1929) reported inhibition of growth following thyroidectomy in young *Lacerta* and Giusti (1931), on the basis of observations on a single thyroidectomized turtle (*Clemmys*), noted a similar retardation. On the other hand Krockert (1941), also on the basis of a single experimental animal, found that feeding pig thyroid gland to a young python resulted in significant growth inhibition as compared with a control. Wilhoft (1958) suggested that histological evidence of increased secretory activity in the thyroids of young *Sceloporus* is related to growth as well as to the time of exposure to optimal temperatures.

The relation of thyroid function to growth and differentiation during embryonic stages has been studied by Dimond (1954) for the turtle *Chelydra*. Developing eggs were treated with thiourea solutions either by direct injection through the shell or by raising the eggs on cotton soaked in these solutions so as to permit gradual absorption. With optimal concentrations and periods of treatment definite inhibition of thyroid activity was produced as indicated by the characteristic histological response to the goitrogen. When such inhibition was effected the development of the embryo was clearly modified. Growth rate was decreased, abnormalities of the carapace appeared, hatching was greatly delayed, and retraction of the yolk sac, which normally occurs at hatching, failed to take place. Thyroidectomy of pregnant females of *Lacerta* some six to eight weeks before the time for egg laying may result in the death of the embryos or, in cases where the eggs are laid normally, in inability of the young to hatch (Eggert, 1933). It seems clear that in these reptiles, as in birds, the thyroid is important in certain aspects of late embryonic development and particularly in relation to the hatching process.

THE THYROID AND METABOLISM

Although the role of the thyroid hormone in the control of metabolic rate in warm-blooded vertebrates is well known, unequivocal evidence for a similar function in poikilotherms is still lacking. The few papers relating to this problem in reptiles are nearly all concerned with lizards.

Weigmann's (1932) account of seasonal changes in thyroid histology in *Lacerta* was accompanied by a study of seasonal differences in metabolic rate. Measurements of CO_2 production at two different temperatures, 15° and 29° C., were made on freshly collected specimens for each month in the year. The metabolic activity, at either temperature, was found to be higher in summer than in winter. Moreover the curve, at either temperature, shows a marked rise in the spring after hibernation. Weigmann considered the spring rise as related to reproductive activity and not directly to the thyroid, but the decrease in metabolic rate in winter was regarded as at least partly the result of decreased thyroid activity.

Eggert (1933) interpreted the effects of the thyroid on shedding of the skin in *Lacerta* as being brought about through control of total metabolism. He maintained that the gas exchange of the animal is markedly lowered as a result of a low level of thyroid activity just before shedding. However this hypothesis was not tested by any measurements of metabolic rate. Eggert (1936a) also concluded that the ultimate death of thyroidectomized lizards is ascribable to a decrease in a number of metabolic processes which causes gradual weakening of the animal.

Experiments involving direct measurement of oxygen consumption in lizards indicate that the thyroid does not affect oxidative metabolism. Maher and Levedahl (1957), using a modified Warburg-Barcroft system, measured oxygen consumption in normal, thyroidectomized, and thyroxin-treated animals at different temperatures and at different seasons. They found no significant differences between controls and experimentals in either group.

Lizards (*Sceloporus*) kept for some weeks at widely differing environmental temperatures show differences in thyroid histology which indicate a great increase in thyroid activity at high temperature (35° C) (Wilhoft, 1958). Whether this is simply one aspect of a general rise in physiological activity or is itself partly responsible for an increase in metabolic rate remains to be ascertained.

Krockert (1941) ascribed a loss of weight in a thyroxin-treated *Python* to increased metabolic rate. However, Drexler and von Issekutz (1935) found no change in oxygen consumption in turtles given thyroxin or thyrotrophic hormone and isolated turtle heart also fails to respond to thyoxin (Harvey and MacRae, 1931). On the other hand, blood drawn from alligators given previous treatment with thyroxin shows a higher oxygen consumption than does the blood of controls (Hopping, 1931; Scott, 1935). The acid-base balance of the blood is also affected by the thyroxin treatment. Destruction of thyroxin

in the blood of the alligator is apparently very slow; the increase in oxygen consumption is still demonstrable six months after thyroxin injection.

The Thyroid and Ecdysis

In the Squamata, lizards and snakes, which undergo periodic ecdysis or shedding of the outer layer of the skin, a relation of thyroid function to this process is strongly indicated. Curiously enough, however, the thyroid hormone seems to stimulate ecdysis in one group and inhibit it in the other.

Drzewicki (1926) was the first to report that thyroidectomy in lizards (*Lacerta*) results in a cessation of molting. In subsequent papers (1927, 1929) he described in detail the histological changes in the skin following thyroid removal. He reported that the horny layer of the skin is formed continuously in thyroidless animals and the periodic formation of a border sheet (stratum terminativum) fails to occur. For this reason the outer cornified layers do not separate off but pile up to form a thick, rough, wrinkled covering over the whole body. This even involves the eyes, the conjunctival epithelium becoming horny and many-layered so that the animals are usually blind within 3 to 5 months.

Drzewicki's findings were not confirmed by Noble and Bradley (1933) for the lizard *Hemidactylus*. Neither hypophysectomy nor thyroidectomy causes cessation of ecdysis in this animal although either operation does result in a lengthening of the period between molts. Thyroxin injections cause a return of the molt to its normal periodicity. However, thyroxin administration to unoperated specimens does not decrease the periods between molts. Noble and Bradley noted that Drzewicki had used only a small series of lizards and suggested that his results might have been due to poor health in his animals.

However, Eggert's (1933, 1936a) exhaustive investigations for three different species of *Lacerta* fully confirmed Drzewicki's conclusions for this genus and further demonstrated that definite changes in thyroid histology are correlated with specific phases of epidermal differentiation and ecdysis. Active formation of new epidermis occurs during about the last third of the interval between molts. Within a few days after the beginning of this new growth the thyroid begins a decrease in epithelial height and shows other indications of declining secretory activity. Cornification of the old uncornified epidermis as well as of the newly formed sheets of cells occurs during this time. Colloid storage is at its maximum in the thyroid during the period when the loose horny sheet is differentiating. The process of molting, which takes only a few hours, then follows. With the beginning of molting the thyroid shows increased production of new colloid and release of stored colloid, epithelial height increases and chromophobe droplets become numerous. By the end of molting most follicles are in the active phase and all follicles appear active within 3 - 4 days after ecdysis. Thyroidectomy causes complete cessation of shedding

but homoplastic implantation of thyroid tissue into the back muscles of thyroidectomized animals is followed by at least one or two successful molts.

Sembrat and Drzewicki (1935, 1936) in further experiments with *Lacerta* showed that in thyroidectomized animals which have ceased to shed, a new molt can be induced by implantation of thyroid material from the shark *Scylliorhinus.* They point out that the shark itself never undergoes a molting process. The ability of its thyroid secretion to induce ecdyses in lizards may be considered to support Eggert's conclusion that the effect is due to a general influence on metabolism rather than to any specific principle related to molting.

Adams and Craig (1950a) also confirmed the fact that thyroidectomy results in cessation of molts in *Lacerta.* They found, however, that administration of goitrogens (thiourea, thiouracil) did not affect molting. It seems clear that this was due to insufficient dosage of the goitrogens for the thyroids of these treated animals also failed to show any significant effects. In another lizard (*Anolis*) Adams and Craig (1949) did obtain thyroid hyperplasia after goitrogen administration but unfortunately did not have sufficient data to make conclusions on molting. Ratzersdorfer, Gordon, and Charipper (1949) also found that thiourea injections induce thyroid hyperplasia in *Anolis* and that this reaction can be prevented by simultaneous administration of thyroxin. In their experiments the thiourea treatment did not cause cessation of molting or even affect the interval between molts although they did note an increase in the time required for the actual molting process.

It seems quite clear that the process of ecdysis is strongly influenced by thyroid activity in lizards. However, in view of the differences reported for the three genera which have been studied, more extensive investigations for still other genera are highly desirable.

Present evidence indicates that the thyroid influence on molting in snakes is the opposite of that in lizards. Schaefer (1933) reported that either hypophysectomy or thyroidectomy causes an increase in molting activity in garter snakes. Operated animals were found to shed 5 or 6 times during the period when similarly fed controls shed only once. Feeding of desiccated thyroid tissue to hypophysectomized or thyroidectomized specimens prevented shedding. Schaefer maintained that the effect of the thyroid on ecdysis cannot be explained merely on the basis of a lowering of the metabolic rate, for animals kept at hibernating temperatures for several months did not shed at all.

Krockert's (1941) experiment on thyroid-feeding in *Python* is in agreement with Schaefer's findings. His thyroid-treated animal shed only 4 times in 16 months whereas control and pineal-fed specimens molted 8 times during this period. The thyroid-fed snake returned to a normal shedding rate about year after cessation of treatment.

The experiments of Halberkann (1953, 1954a, b) demonstrated

these same relations for *Natrix*. Thyroxin or TSH administration inhibits shedding while treatment with a thyroid-inhibiting drug (methylthiouracil) causes an increase in the number of molts.

Miscellaneous Effects of Thyroid Hormone

Eggert (1933, 1936a) has shown that complete thyroidectomy in *Lacerta* results in ultimate death after periods of 3 to 8 months. The main cause of death is an anemia attributable to a marked decrease in blood-forming activity in bone marrow. There is also a gradual decrease in activity and appetite with a mobilization of fat reserves. The animals finally refuse to eat and die in a cachetic condition. All of these effects can be alleviated or prevented by homoplastic thyroid implantation or by thyroxin administration. In *Hemidactylus,* on the other hand, Noble and Bradley (1933) found that thyroidectomized animals show no differences in behavior and no increase in death rate as compared with controls. The survival time of their specimens is not given, however.

A relation between the thyroid and blood formation has been reported by Charipper and Davis (1932) for the turtle *Pseudemys*. They found that thyroxin administration results in increase in the leucocyte count by stimulating granulocytopoietic centers so as to cause an increase in the number of young eosinophils. This they considered analogous to a left-hand deflection of the polymorphonuclear count previously reported for amphibians, birds, and mammals

Thyroid effects on behavior are mostly concerned with hibernation and breeding activity and these have already been considered. Evans and Clapp (1940) noted that territorial behavior, the urge to defend a specific home territory, and general pugnacity are increased in both sexes of *Anolis* by injection of thyroxin or TSH. Krockert (1941), on the basis of thyroid feeding of a single young python, reported a great increase in irritability as compared with an untreated and a pineal-fed litter-mate.

Summary

The reptilian thyroid is always a well-defined encapsulated gland. In turtles, snakes, and *Sphenodon* it is unpaired; in Crocodilia it is markedly bilobed. Among lizards there is wide diversity in thyroid morphology and position. Embryonic origin and early development of the gland show no unusual features.

The fundamental histology of the reptilian thyroid agrees with that found in other amniotes. Seasonal changes in histology both in relation to temperature and breeding season are of particular interest. Studies of these matters are available for several lizards but further investigations are much needed for both hibernating and non-hibernating lizards and especially for snakes, turtles, and crocodilians. In lizards it has been demonstrated that the thyroid shows well-defined histological changes in relation to differentiation and shedding of

the horny layer of the skin. In view of the fact that thyroid function also plays a role in ecdysis in snakes, similar studies should be carried out on representatives of this group.

Pituitary control of thyroid activity by means of thyrotrophic hormone is well demonstrated for reptiles as for other vertebrates. Response to various antithyroid agents seems to differ markedly in different reptiles, however, and this subject deserves further study. The reported effects of thyroidectomy upon other endocrine organs such as parathyroid, thymus, ultimobranchial body, and gonad also require more extensive investigation.

There is some evidence that the growth rate of reptiles, both at embryonic and post-embryonic stages, is affected by the thyroid hormone. More critical studies on a wider variety of forms will be necessary before the nature and extent of this effect can be defined. The importance of the thyroid in certain aspects of late embryonic development and hatching has been demonstrated for one turtle and one lizard. Again the need for more comprehensive investigations is obvious.

As is the case for other cold-blooded vertebrates, the significance of the thyroid in metabolism of reptiles is far from clear. Most authors who have assumed that the reptilian thyroid affects metabolic rate have based their conclusions on circumstantial evidence. Only experiments involving direct measurement of appropriate metabolic processes can solve this problem.

The fact that the thyroid plays an important role in ecdysis in *Lacerta* is well established. However, the representatives of two other genera of lizards which have been studied show rather marked differences in response. Moreover, the effect of the thyroid on molting in snakes seems to be just the opposite of that in lizards. Further experiments on this matter are much needed in both groups.

The use of radioiodine as a tool in study of thyroid function is a promising technique which remains almost entirely unexploited for reptiles. Investigations concerning iodine uptake and turnover at different seasons, under different environmental conditions, at different phases of the reproductive and molting cycles, and under various treatments would go far to elucidate some of the unsolved problems mentioned above.

The reptiles occupy a unique position among vertebrates as the only cold-blooded amniotes. The number of types of reptiles readily available as experimental animals is gradually increasing. Recent advances in histological techniques and experimental methods have largely superseded many of those used in the earlier investigations reviewed above. General interest in reptilian physiology seems to be on the rise. It is to be expected that within a short time these factors will combine to provide a considerable increase in our knowledge of the reptilian thyroid.

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Postmetamorphic Growth in Anurans[1]

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Knowledge of the rate of growth and time of sexual maturity is necessary in analyzing the age structure, survival rate and reproductive potential of anuran populations. Growth rates of transformed anurans have been determined in three ways, depending on measurements of (1) preserved materials, (2) captive individuals, and (3) individuals, either marked, or in large samples taken from the same natural population at different times during the same growing season.

Except for the first two or three-year classes, the identification of age groups is impossible in samples from different, or even the same, populations. Nevertheless, Wright (1932) presented growth rates of 19 anuran species from Georgia based primarily on size-frequency distributions. Subsequent analyses of anuran growth rates in Florida (Pearson, 1955; Hamilton, 1955) have confirmed some of Wright's conclusions. On the other hand, Wright's (1920, 1932) estimates of growth in *Rana catesbeiana,* based on northern material, do not agree with findings of later workers (Raney and Ingram, 1941; Ryan, 1953).

Growth rates of captive individuals, as reported by Flower (1925, 1936), Cowan (1941), and Wilson (1950), are of questionable validity as estimates of growth rates of individuals under natural conditions.

There are few studies of growth under natural conditions. Force (1933) and Bannikov (1950) depended on modal size differences in mass samples collected at the same locality at different times. This technique reveals the average growth rate but tends to obscure the magnitude of individual variation. Furthermore, this method is most effective when the growth rate is fast enough to give a recognizable modal difference within a period of a few weeks. The time element may be critical—unless the entire population is restricted to a small area, movements or ecological shifts may modify the age structure of the second sample (with reference to the first) and invalidate the whole procedure.

Other studies have been based on the growth of marked *individuals* in a natural population. Growth data are based on subsequent recaptures and remeasurements of these marked individuals (*e.g.,* Hamilton, 1934 and 1955; George, 1940; Raney and Ingram, 1941; Raney and Lachner, 1947; Blair, 1953; Pearson, 1955 and 1957; Fitch, 1956a and 1956b; Jameson, 1956; Martof, 1956; and Turner 1957). The snout-vent (or snout-urostyle) length is usually measured and is difficult to determine accurately. Ryan (1953) and Hamilton (1955) made several measurements of each individual and used a mean value, achieving greater accuracy. Pearson (1955) showed that some other

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TABLE I.—Features of growth rates of anurans as revealed by 14 studies of natural populations (all sizes in millimeters and *approximate* — may represent average or central value of entire range).

Worker	Species	Locality	Maximum size ♂	Maximum size ♀	Size at transformation	Growth to hibernation	1st full season following transformation	2nd full season	3rd full season	Time to sexual maturity (year after transformation) ♂	Time to sexual maturity (year after transformation) ♀
Force (1933)	*Rana pipiens*	Michigan	80?		32	5?	10	7	—	4	4
Ryan (1953)	*Rana pipiens*	New York	82	92.5	25	22	20	16?	slight	1-2	1-2
Raney & Ingram (1941)	*Rana catesbeiana*	New York	—	155	45	8	40	30	15	2-3	2-3
Ryan (1953)	*Rana catesbeiana*	New York	—		52	10+	45	—	—	2	2
George (1940)	*Rana catesbeiana*	Louisiana	171	184	40	29	60	25?	—	2	2
Ryan (1953)	*Rana clamitans*	New York	90	98	32	22	31	slight	—	1-2	1-2
Martof (1956)	*Rana clamitans*	Michigan	103	105	32	6	28	17	5.5	1-2	1-2
Turner (1957)	*Rana pretiosa*	Wyoming	61	72	16	9	10	6.5	5.5	4	5-6?
Hamilton (1934)	*Bufo terrestris*	New York	—		10	20	40	18?	slight	3?	3?
Raney & Lachner (1947)	*Bufo terrestris*	New York	100	115	10			5?	slight?	2	2
Blair (1953)	*Bufo valliceps*	Texas	—		10	—	70+			1	1?
Hamilton (1955)	*Bufo quercicus*	Florida	26+	30+	7.5	11	9	slight		1	2
Pearson (1955)	*Scaphiopus holbrooki*	Florida	77+	71+	10	—	32	8	3	1-2	1-2
Jameson (1956)	*Hyla regilla*	Oregon	44?		14	7	14			1	
Fitch (1956a)	*Gastrophryne olivacea*	Kansas	37?	42	15	5-13*	11-5*			1-2	1-2
Bannikov (1950)	*Bombina bombina*	Near Moscow, Russia	56?		17	5	13	10	slight	2	2

* Two different broods.

TABLE II.—Growth during the first and second years following transformation and its relationship to maximal size in 10 anuran species

Species	Difference between maximum size and size at transformation (mm)	Growth by end of first full year after transformation	% of total growth	Growth by end of second full year after transformation (mm)	% of total growth
Rana pipiens					
(Force, 1933)	48	15	31	22	46
(Ryan, 1953)	60	42	70	58?	97?
Rana catesbeiana					
(George, 1940)	138	89	65	114?	83?
(Raney & Ingram, 1941)	105	48	46	78	74
Rana clamitans					
(Ryan, 1953)	62	53	85	slightly more	?
(Martof, 1956)	72	34	47	51	71
Rana pretiosa					
(Turner, 1957)	50	19	38	26	52
Bufo terrestris					
(Hamilton, 1934; Raney & Lachner, 1947)	97	60	62	78?	80?
Bufo quercicus					
(Hamilton, 1955)	20	19	95		
Hyla regilla					
(Jameson, 1956)	30?	21	70?		
Gastrophryne olivacea					
(Fitch, 1956)	25	17	68	21	84
Scaphiopus holbrooki					
(Pearson, 1955)	64	32	50	8	63
Bombina bombina					
(Bannikov, 1950)	38?	18	46	28	74

body dimension may be used as an index of growth. He calculated growth rates of *Scaphiopus holbrooki* from measurements of the width of the head, and related this dimension to increase in body length.

RESULTS OF STUDIES OF NATURAL POPULATIONS

Table I summarizes features of growth in anurans revealed by 14 studies of natural populations.

General patterns of growth.—Because of the different sizes of the species involved, it is impossible to compare the absolute increments of growth. However, a proportion may be derived to permit comparison. If a "maximum" size, expressing the approximate limit of growth, is established for members of each population (a mean value when there is marked sexual dimorphism), the difference between this value and the average size at transformation approximates the maximal amount of growth. Growth for any given period may then be expressed in comparable terms, as percent of total growth. The patterns of growth exhibited are diverse, but because the forms in-

volved represent 6 different families of anurans this variation is not surprising (Table II). In the American toad the transformation size (*ca.* 10 mm) is small when compared to the maximal size (over 100 mm), but in the population of *Rana clamitans* studied by Ryan (1953) the transformation size (32 mm) is about 1/3 of the maximal adult size (90-98 mm). Hence, while the significance of the interspecific comparisons in Table II is uncertain, it *is* pertinent to compare the growth of members of different populations of the same species. Just why there is such variation in growth rates in different populations of *Rana pipiens, R. catesbeiana,* and *R. clamitans* is not presently known, though the roles of temperature and length of growing season are undoubtedly important. George (1940) showed that in Louisiana populations of *Rana catesbeiana* the tadpoles require but one season to transform (as opposed to 2 or 3 in New York), and that postmetamorphic growth and the attainment of sexual maturity are comparably accelerated in the south. It is tempting to ascribe this condition simply to differences in duration of growing season. However, Wright's (1932) data imply that *Rana clamitans* grows more rapidly and to a greater size in New York than in Florida.

These problems resemble those encountered in studies of the developmental rate of anuran embryos and larvae from different populations of the same species. Most of the comparisons of embryonic and larval development in conspecific populations have involved *Rana pipiens* (Moore, 1944; Volpe, 1954, 1957b; Ruibal, 1955), but several species of toads have also been studied (Volpe, 1953, 1957b). The above workers have shown that there are differences in the developmental rate of embryos and larvae, apparently associated with varying temperature regimes or other environmental factors (*e.g.,* rate at which temporary breeding sites dry). As far as postmetamorphic growth is concerned, those adaptations governing rate of development at varying temperatures are most pertinent. The basic idea, when temperature adaptations are involved, is that the embryos of cold-climate populations (*i.e.,* those at high latitudes or high altitudes) are adapted to develop relatively rapidly in cold water (12-15°C), while embryos of warm-climate populations mature relatively more rapidly at water temperatures around 25-30°C. However, at least one cold-climate population has been studied, the embryos of which do not show this sort of adaptation (Ruibal, 1955:333). Here it appears that the whole mechanism of development is retarded by lower temperatures with no counteracting adaptation. These features of embryonic and larval development are reviewed here because of the likelihood that postmetamorphic growth may be similarly influenced (see also Volpe, 1957c:360). However, temperature adaptations related to postmetamorphic growth are not apt to be as striking as those shown to be involved in embryonic development. In most anuran populations the eggs and larvae are the stages in the life cycle against which selective forces operate most rigorously. Because there has been no pertinent experimental work on postmetamorphic growth only speculation is possible. Probably some variable anuran species are adapted for rapid

growth and sexual maturation even in cold climates. Other species may grow at rates simply correlated with temperature and length of growing season. What little is known of bullfrog populations seems to fit this picture.

Future investigations might involve the transplanting of marked individuals from one population to another population of the same species existing under different environmental conditions. A comparison of the growth of the transplants with the members of the undisturbed population might afford clues as to the interaction of the genetic and environmental determiners of growth rate.

In any event there are two extreme patterns of growth (Fig. 1). Most of the growth may take place during the same season as transformation (*e.g., Rana clamitans* in New York, *Bufo quercicus* in Florida, *Bufo valliceps* in Texas), with much smaller increments added in successive years. Or the early growth may be more modest and the later increments, though smaller than the initial growth, are not as drastically reduced as in the preceding examples (*e.g., Rana pipiens* in Michigan and *R. pretiosa* in Wyoming).

Sexual maturation.—The time of sexual maturation is of importance in evaluating the reproductive potential of a population of known age composition. Some ambiguity is associated with the term "sexual maturity," for the phrase has been used both to indicate actual

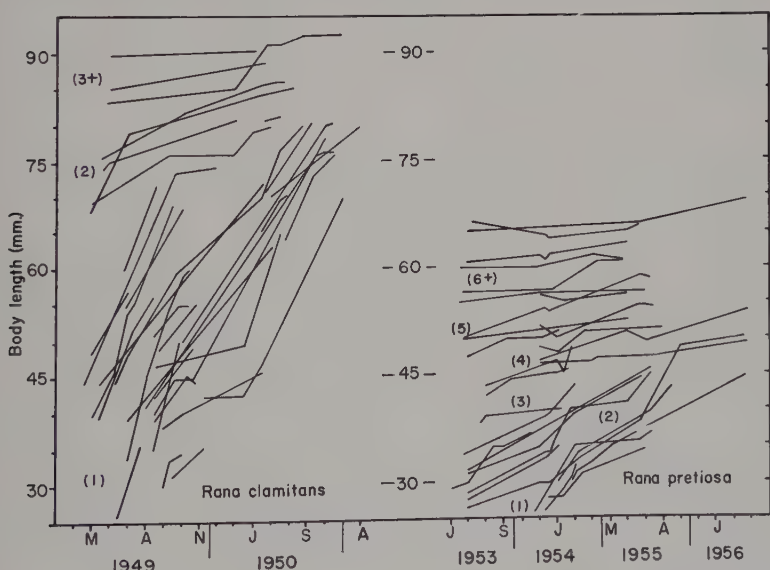

Fig. 1.—Growth rates in *Rana clamitans* and *Rana pretiosa*. Growth records of marked individuals are portrayed as revealed in studies extending over 3 and 4 seasons respectively. Figures in parentheses indicate age-classes. (From data in Ryan, 1953, and Turner, 1957.)

participation in breeding activities and to imply the presence of mature gametes in the gonads. Table I indicates the time at which breeding activities are commenced. The year after transformation is recorded —not the chronological age, which is ordinarily less by 3 to 6 months. Some studies revealed that the first breeding activity might occur in either the first or second season after transformation. In rapidly growing species these differences are associated with the time of transformation, *i.e.,* early or late in the growing season. However, in *Rana pretiosa* in Yellowstone Park, where the pre-reproductive life span is so long that slight age differences within the same year-class are unimportant, differences in time of first breeding in females probably are due to variation in the rate of maturation (Turner, 1957).

Variation in growth during different growing seasons.—It has been assumed that, in the same population, anurans of any given age grow a specific amount in one growing season. If workers have suspected, for example, that growth might be exceptionally fast one year and unusually slow the following year, such feelings have been unexpressed because of the difficulty in establishing such differences. It is almost impossible to attack this problem by comparing a limited number of individual growth records. The amount of inherent individual variation is apt to be greater than minor size differences caused by fluctuations in environmental conditions; hence large samples must be available for comparison. Because the growth rates of mature anurans are very slow, such differences can only be demonstrated in the first few years after transformation. In my work with *Rana pretiosa* I suspected that the frogs transforming in 1953 grew a few millimeters more during the summer of 1954 than the frogs which transformed in 1952 grew during 1953. The difference was not statistically significant, but in future studies some attention might be directed to this problem. Drastically differing climatic conditions in successive years could influence the rate of growth sufficiently to complicate the apparent age structure of the population insofar as the year-class size-limits are concerned. Ordinarily, however, there is an inherent capacity for growth in anurans of a given age, which overrides environmental influence. For example, Fitch (1956a, 1956b) reported on the growth of two broods of *Gastrophryne olivacea* transforming during the summer of 1954. One group of frogs transformed in June (average size *ca.* 15 mm), and by the end of August had attained an approximate size of 26 mm. By the middle of October these frogs were about 28 mm in length. Members of the other group transformed in late August and attained an average size of 22 mm by the second week in October. In other words, the second (and younger) group grew about 7 mm over the same 6-week period during which the frogs that transformed in June grew about 2 mm.

Seasonal rate of growth.—Studies of growth during one growing season have shown that, except in *Scaphiopus holbrooki,* most growth occurs during one period of the season. This has been most clearly

demonstrated by Martof (1956) for *Rana clamitans* and Turner (1957) for *R. pretiosa*. Martof showed that growth is most rapid during July and that the seasonal growth rate is positively correlated with the number of hours above 60°F. Similarly, in *R. pretiosa* from about 33 to 50 percent of the seasonal growth occurs during a two-week period in July. Ryan (1953) found a comparable condition in young *R. clamitans* in New York, but concluded that the growth of the oldest frogs occurred in the beginning of the growing season. Also, in the *Gastrophryne* observed by Fitch, the frogs transforming in June grew about 11 mm in the 7 weeks following transformation, while those transforming in August grew only 7 mm in the 7 weeks following *their* transformation. Fitch attributed these differences to the higher midsummer temperatures under which the former group developed. Jameson (1955) stated at one point that *Syrrhophus marnocki* grows "faster through the fall and winter months," and in another that "the rate of growth was found to be greater in the spring and summer months. . . ." The latter statement seems more correct. Such variation is the rule even when there is no winter hibernation. *Rana catesbeiana* grows throughout the winter in Louisiana but at a reduced rate (George, 1940). Pearson (1955) concluded that the growth rate of *Scaphiopus holbrooki* in Florida is *not* influenced by the time of year. This unusual condition is probably associated with the habits of these toads. Pearson points out that the toads remain in their burrow most of the time, emerging to feed only about 30 times a year, and that such excursions occur with equal frequency at any season. Possibly these forays are so brief that seasonal differences in the environment do not influence growth rate.

Differential growth of the sexes.—In general, for anuran species studied, the females attain larger sizes than the males (Table I). However, different populations of the same species may vary in this respect. For example, Ryan (1953) found clear-cut size dimorphism in the New York population of *Rana clamitans*, but Martof (1956) maintained that in Michigan there are no maximal size differences between males and females. The time at which size differences first appear varies. In New York, marked differences in male and female *R. clamitans* are apparent during the first season following transformation (Ryan, 1953). The same is true of *Gastrophryne olivacea* in Kansas (Fitch, 1956a), and some other forms. However, Turner (1957) could not demonstrate significant differences in the mean size of 4- and 5-year old male and female *Rana pretiosa*. Furthermore, the males of *Scaphiopus holbrooki* are larger than the females, so size dimorphism does not always involve larger females.

Size dimorphism may arise simply as a result of more rapid growth by the larger sex (Ryan, 1953; Pearson, 1955; Fitch, 1956a). However, if one sex outlives the other, the oldest (and largest) members of the population will be of the same sex. The possible contribution of differential mortality to size dimorphism has been suggested by Turner (1957).

Individual variation.—Variation in the growth rates of individuals of the same age has been revealed in all previous studies of anuran growth. Hence, the size-limits of any one age-class may be quite broad—especially in the youngest individuals. Some of this spread represents differences in size at transformation or slight differences in age within the same age-class (resulting from differences in time of transformation). For example, the size of one-year old *Rana catesbeiana* and *R. clamitans* may vary as much as 30-40 mm (based on data of Ryan, 1953; George, 1940). However, even in a cohort of frogs or toads of identical age and size a certain amount of variation in size would soon obtain. *Rana pretiosa* in Yellowstone Park transforms during a few weeks in August and early September (thus minimizing age differences in any one age-class) and the extreme sizes of the early age-classes differ by only about 10 mm (Turner, 1957). The size-limits of some of the early age-classes in ranids are indicated in Table III.

In general the total range of size within the age-classes seems to decrease with greater age, but this impression may be the result of bias in analysis. Anderson (1954) pointed out that *Gastrophryne carolinensis* transforms from May until October, producing an initial age-class of considerable range in size the following spring. However, he stated that this effect seems to be diminished in older individuals, implying that individuals tend to approach more closely a modal size with greater age.

Growth rate and population density.—Population density may influence growth. Pearson (1955) showed significantly different growth rates in two populations of *Scaphiopus holbrooki* of different density. The more dense population grew more slowly. This problem has not been investigated by other workers, and in just what manner greater densities operate to slow growth is not known. The retardation may

TABLE III.—Limits of size in 4 species of the genus *Rana* during the first 2 to 4 years following transformation as revealed by studies of 6 natural populations (when two ranges are given, one is early in the growing season, the other later in the same season).

Species	Age-class size-limits (mm) 1	2	3	4
Rana pipiens				
(Force, 1933)	35- 50?	52- 61?		
R. clamitans	33- 60	72- 79	83- 90	
(Ryan, 1953)	40- 73	76- 82	84- 90	
R. pretiosa	20- 30	30- 39	37- 45	46- 49
(Turner, 1957)	23- 32	30- 40	38- 46	45- 50
R. catesbeiana	44- 82	101-133		
(George, 1940)	101-120			
(Raney & Ingram, 1941)	67- 90	82-110	113-126	125-139
(Ryan, 1953)	55- 92			
	64- 90			

be simply the result of intraspecific competition for food. Whether slight variations in density within *one* population (associated with contagious dispersion) might contribute to individual variation within the same population is not known.

Loss of length.—Apparent loss of length has been reported by almost all investigators of anuran growth. This problem is an unavoidable consequence of measuring the body length of an animal as pliable as a frog or toad. Such apparent losses appear more commonly in larger individuals. Raney and Lachner (1947) found apparent shrinkages to be relatively common in large toads, and Martof (1956) and Turner (1957) encountered similar results in work with *Rana clamitans* and *R. pretiosa*. Ryan (1953), who performed 3 measurements and averaged them, reported few cases of loss of length; this supports the conclusion of Raney and Lachner that such "losses" are the result of errors in technique. However, Martof suggested that the apparent loss of length in green frogs (most commonly between October and April) might be associated with changes in the condition of the frog related to hibernation—especially if measurements of body length were made from the tip of the snout to the anterior lip of the cloaca instead of to the end of the urostyle. In *Rana pretiosa* it was found that apparent losses were more common in males of breeding age, and occurred between May and some subsequent time in the season (Turner, 1957). If a dimension other than the snout-urostyle length of a frog is actually measured, one might expect some "shrinkage" of breeding males following nuptial activities.

DISCUSSION

Volpe (1957c), in discussing studies of anuran population (including individual growth rates) comments:

> There are few precise and detailed studies of these factors in natural populations. In the literature may be found an array of desultory field observations, much of which cannot be integrated into a comprehensive picture.

There is considerable truth in these remarks. A clear-cut rationale for studies of anuran growth has been largely lacking, although Cagle (1956) has set forth a general program for amphibian life history studies.

If we wish to describe growth, as it occurs under natural conditions, I see no feasible alternative to studies of natural populations. Large enclosures might be used (see Pearson, 1955) but the use of cages or fences always introduces an element of artificiality, which is most extremely expressed in records of the growth of pets (*e.g.*, Cowan, 1941; Wilson, 1950). However, well-designed experiments could be of value in studies of growth, especially in determining the influence of such factors as age, sex, population density, temperature, food supply, etc. The experiments should be replicated with subjects from one population, with provisions for control of environmental variables. In field studies individuals should be marked by a tattooing device as

described by Kaplan (1958, 1959). Toe-clipping is not always reliable, especially when studies of several years' duration are involved. There is always some regeneration of excised toes, sometimes enough to cause uncertainties. Even more serious, toes are lost accidentally; unmarked individuals may appear to be marked and marks may be changed owing to such losses. There is a tendency to explain what appears to be exceptional growth as resulting from misidentifications. Emphasis should be laid on the accumulation of a large number of individual growth records. Three measurements involving different frogs will be more instructive than the mean of three measurements of the same individual. The somewhat improved accuracy of the latter technique does not justify the additional time necessary.

Aside from the theoretical value of growth rates, there are two ends served by such information. The first of these is predicated on what might be called the descriptive approach, and is of interest to the population ecologist—namely the age structure and effective breeding size of a population and the fluctuations in these attributes. Information on the attainment of sexual maturity, differential growth of the sexes, and individual variation is subservient to, and contributes to, the major problem: that of describing the age composition of the population and its breeding structure. Such parameters as survival rate, reproductive potential and rate of population growth may then be estimated. The second end is related to causal aspects of growth. Here growth rate and its variations are part of a larger picture involving the influence of age, sex, population density, temperature, food supply and other environmental factors.

Summary

The growth rate of anurans, maximal size, and the time at which sexual maturity is attained may vary between different populations of the same species. In some populations studied most of the growth takes place within a year or two after transformation; after this time growth is slight. At the other extreme are species in which the postmetamorphic growth is spread out over some years, so that the annual increments are not so markedly reduced. Seasonal variation in growth is the rule, even when the growing season is not interrupted by hibernation. Size dimorphism probably arises as a result of differential rates of growth by the sexes. Some populations of the same species may show size dimorphism, others not. Variation in the size of anurans of the same age arise because of differences in time of transformation (within the same season) and because of individual variation in growth rates.

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A Study of Eleocharis, Series Ovatae

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In his latest treatment of the genus, Svenson (1957) subdivided *Eleocharis* into eight morphological series, the fourth being Series Ovatae. Members of this series are cespitose annuals or rarely perennials that possess smooth, biconvex achenes that are glistening brown when mature, with compressed lamelliform tubercles, and 2- to 3-cleft styles.

Svenson (1927, 1939, 1957), in his monographic studies, maintains four species, with three of them (*E. obtusa, E. ovata,* and *E. engelmanni*) from Illinois. The fourth species, *E. lanceolata,* with ovoid, acute scales and lanceolate spikelets, is apparently not found in Illinois. In addition, the bristleless *E. engelmanni* f. *detonsa* is cited from Illinois.

Gilly (1946), in his work on Iowa Cyperaceae, noted that intergrading forms occur between *E. obtusa* and *E. engelmanni,* even to the extent that typical achenes of both may be found on the same specimens. He felt that the two taxa should not be considered distinct species, but that *E. engelmanni* should be considered a variety of *E. obtusa.* He therefore proposed *E. obtusa* var. *engelmanni.* Fernald (1950), Jones (1950), and Gleason (1952) have maintained *E. obtusa, E. engelmanni,* and *E. ovata* distinct in Illinois.

Svenson (1953) in his detailed work on the obtusa-ovata complex states that many intermediate forms do exist where the variations come in contact or where unusual environments persist. He also stresses the need for further investigation within this group.

While studying the genus *Eleocharis* in Illinois, it became apparent to the authors that specimens determined previously as *E. obtusa, E. engelmanni,* and *E. ovata* were part of a confusing complex. As a result of this, analytical studies of morphological characters of these specimens were carried out. This paper presents these data, and through the interpretation of these data, offers a systematic treatment of these taxa.

Analysis of Characters

Eleocharis obtusa, E. engelmanni, and *E. ovata* share several characteristics in common. They are all cespitose annuals which range from 3-50 cm tall, with spikelets ovoid or oblong, obtuse to acute, 2-16 mm long, with appressed scales ovate or oblong, with similar coloration. The achenes are obovoid, smooth, yellow or deep brown, 0.9-1.0 mm long.

In their extreme conditions, all three entities appear rather distinct. *Eleocharis obtusa* has ovoid or rarely oblong spikelets which are obtuse to acute. The achenes average 0.9 mm long and 0.8 mm wide, with a tubercle which averages 0.3 mm long and 0.6 mm wide.

The width of the tubercle is more than two-thirds the width of the achene, while the height of the tubercle is more than one-fourth the height of the achene. The bristles are longer than the tubercle, or rarely lacking.

Eleocharis engelmanni has oblong or rarely ovoid spikelets which are obtuse to acute. The achenes average 1.0 mm long and 0.8 mm wide, with a tubercle which averages 0.2 mm long and 0.7 mm wide. The width of the tubercle is more than two-thirds the width of the achene, while the height of the tubercle is one-fourth, or less than one-fourth, the height of the achene. The bristles may be lacking or as long as the achene.

Eleocharis ovata has ovoid or very rarely oblong, acute or rarely obtuse spikelets. The achene averages 1.0 mm long and 0.7 mm wide, with a tubercle which averages 0.3 mm high and 0.4 mm wide. The width of the tubercle is two-thirds, or less than two-thirds, the width of the achene, while the height of the tubercle is usually about one-fourth the height of the achene. The bristles range from longer than the achene to completely lacking.

The figures obtained in this study for the taxa above are similar to those cited by Svenson (1953).

Specimens which may be considered intermediate are those with the tubercle one-fourth or less than one-fourth the height of the achene and more than one-half the width of the achene with bristles overtopping the achene. The spikelets are ovoid or oblong, obtuse to acute, with achenes averaging 1.0 mm long and 0.8 mm wide, with tubercles averaging 0.2 mm long and 0.6 mm wide.

Summary and Conclusions

Achene size of all taxa considered in this study is essentially the same. On the average, achenes of *E. obtusa* are slightly shorter, while achenes of *E. ovata* are slightly narrower. Tubercles of *E. obtusa* and *E. ovata* are usually higher than those of *E. engelmanni* and the intermediate specimens. Tubercles of *E. ovata* are narrower than those of the other taxa.

The tubercles of *E. obtusa* are more than one-fourth the height of the achene while those of *E. engelmanni* and the intermediate specimens are one-fourth or less than one-fourth the height of the achene. The tubercles of *E. ovata* are two-thirds or less than two-thirds the width of the achene, while the tubercles of the other taxa are wider than this.

The bristles of *E. engelmanni* never exceed the achene and tubercle, while the bristles of the other taxa sometimes may exceed them. It does not seem feasible to recognize the bristleless form because of the variability of the bristles in this series.

Spikelet shape and scale shape appear to be of little taxonomic significance.

Because of the great variation shown by the intermediate specimens, it seems best to treat *E. engelmanni* as a variety of *E. obtusa*.

The first available varietal epithet of *E. engelmanni* is *detonsa* A. Gray. Since we do not feel that var. *detonsa* (meaning bristleless) is distinct from typical *E. engelmanni,* a new combination for all material of *E. engelmanni* must be made. It would be:

Eleocharis obtusa (Willd.) Schultes var. **detonsa** (A. Gray) Drapalik & Mohlenbrock, comb. nov.

Eleocharis obtusa and *E. ovata* are almost identical in appearance except that *E. ovata* has narrower tubercles and generally a smaller, ovoid, acute spikelet. Because of these seemingly tenuous characters, it seems best to relegate *E. ovata* to varietal status under *E. obtusa.* The new combination would be known as:

Eleocharis obtusa (Willd.) Schultes var. **ovata** (Roth) Drapalik & Mohlenbrock, comb. nov.

KEY TO ILLINOIS ELEOCHARIS, SERIES OVATAE

A. Tubercle more than two-thirds the width of the achene; bristles longer than the tubercle to lacking.
  B. Tubercle one-fourth to one-half the height of the achene; bristles longer than the achene, or rarely wanting .... *E. obtusa* var. *obtusa*
  B. Tubercle up to one-half the height of the achene; bristles as long as or longer than the achene, or lacking .... *E. obtusa* var. *detonsa*
A. Tubercle one-half to two-thirds the width of the achene; bristles usually longer than the tubercle .... *E. obtusa* var. *ovata*

ABERRANT INDIVIDUALS

A specimen collected by Virginius H. Chase (No. *138*), identifiable as *E. obtusa* var. *detonsa,* possesses spikelets that are enlarged and flattened at the apex, and tri-cleft as well as simple. A specimen collected by Abney, Dillard, and Mohlenbrock (No. *156*), identifiable as *E. obtusa* var. *detonsa,* possesses a dichotomously branched spikelet, as well as simple ones.

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The Pancreatic Islets of Desert Rodents

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During a recent study of the endocrine organs of the collared lemming, *Dicrostonyx,* a relatively low pancreatic alpha : beta cell ratio was noted in this arctic rodent. It was discovered also that comparative data on the pancreatic islets of rodents in the literature are extremely meager. It seems likely that in at least some species, modifications or specializations in carbohydrate metabolism or utilization associated with climatic adaptations, may be related to modifications in the endocrine glands, especially the pancreatic islets. A survey of the microanatomy of the islets in some North American desert rodents reported here tends to support this belief and contributes data on trends within the Heteromyidae.

I am grateful to John Eisenberg, Dennis Galloway, Richard Graham, John Pun, Mary Taylor, and Alan Ziegler for assistance during the procurement of specimens and to Dr. Seth Benson for aid in the identification of the specimens of *Perognathus.*

Materials and Methods

Approximately 60 specimens, primarily rodents of the family Heteromyidae, were trapped alive in California and Nevada at different seasons and autopsied after death under ether or chloroform anesthesia either immediately after capture or after varying periods of time in captivity. Rapid autolysis of the pancreatic cells after death necessitates immediate fixation of the tissue and prohibits the use of snap-trapped specimens. Pieces of pancreas were fixed in the following fluids for the times indicated: (1) Helly's fluid, without acetic acid, and neutral formalin mixed 9:1 at time of use, 8 or 15 hours (Thomas, 1937); (2) Bensley's (1911) "acetic-osmic-bichromate," 24 hours; (3) Lane's (1907) "alcohol-chrome-sublimate," 4 or 24 hours; (4) 70 per cent ethanol, 24 hours; (5) 9:1 mixture of neutral formalin:isopropanol, 24 hours; (6) 10 per cent neutral buffered formalin (aqueous) (Lillie, 1954), 1 or more months; (7) Bouin's fluid (75 parts saturated aq. picric acid:25 parts formalin:5 parts acetic acid), 24 hours. The tissues were subsequently embedded in paraffin, sectioned at 7 microns, and stained by the following procedures: (1) Bensley's (1911) "neutral gentian"; (2) Gomori's (1941) modification of the azan technique; (3) chrome alum hematoxylin and phloxine (Gomori, 1941); (4) Halmi's (1952) aldehyde fuchsin; and (5) methenamine silver for argentaffin cells (Lillie, 1954, p. 165). Some of the tissues fixed in neutral buffered formalin were washed in water, embedded in 20 per cent gelatin, cut with a freezing microtome and stained for lipids (oil red 0, Lillie, 1954).

RESULTS

The preservation and staining of the parenchymal cells of the pancreatic islets were evaluated primarily in terms of the cytoplasmic contents of the alpha and beta cells of species of *Dipodomys, Perognathus, Microdipodops* and the laboratory rat, *Rattus norvegicus* (Long-Evans and mixed strains). Chromophilic cells other than the alpha and beta types were not found in the heteromyid islets. None of the islets' cells were notable in their lipid content; and no sexual differences, nor differences due to captivity or season were apparent in our limited series. In the islets of both rat (*Rattus*) and kangaroo rat (*Dipodomys*) both alpha and beta cells were pink to dull red after Helly's-formalin fixation and staining with methenamine silver. This is not to be considered a positive argentaffin reaction, however. After other fixatives none of the islets' cells showed cytoplasmic staining with methenamine silver. The azan technique after Bouin's fluid fixation, stained alpha cells' cytoplasmic granules yellow to pale orange and those of the beta cells blue-gray. After other fixatives this technique was not successful in differentially coloring the cell types. Neutral gentian stained the cytoplasmic granules of both alpha and beta cells red to purple. But the differential solubilities of the alpha and beta granules in alcoholic and some aqueous fixatives led to similar variations in the rat and the heteromyid sections of pancreas. The beta granules were reduced and the alpha granules were preserved after alcoholic fixatives. The beta granules were selectively demonstrated best after Helly's-formalin and the granules of both cell types were stained after Bouin's fluid. Chrome alum hematoxylin successfully stained the beta cell granules of heteromyids only after fixation in Bouin's fluid or neutral buffered formalin. And the phloxine counterstain of this procedure stained the heteromyid alpha cell granules best after alcoholic fixatives. The best results in differentially staining these cells in heteromyids were obtained with the aldehyde fuchsin technique following fixation in Bouin's fluid. The alpha cells in this instance have orange cytoplasmic granules and a pale greenish-yellow background and the beta cells have intensely purple granules. The staining of the beta granules with aldehyde fuchsin after Helly's-formalin or formalin-isopropanol fixatives is dependent apparently on species differences as well as on quantitative differences. The beta granules are abundant and densely stained in all specimens of *Microdipodops* after these fixatives; they are moderate in abundance and staining in some specimens of *Dipodomys* and *Perognathus;* and they are rarely and weakly stained in *Rattus norvegicus.*

The most immediately obvious distinction of the heteromyid islets is the central, rather than peripheral or scattered, position of the alpha cells. Within the Heteromyidae there are differences in the degree of central clumping of these cells. The most extreme clumping occurs in *Microdipodops.* This is closely approached by that in *Dipodomys deserti.* In other examined species of *Dipodomys* (*heermanni, merriami, microps, nitratoides, ordi,* and *panamintinus*) the

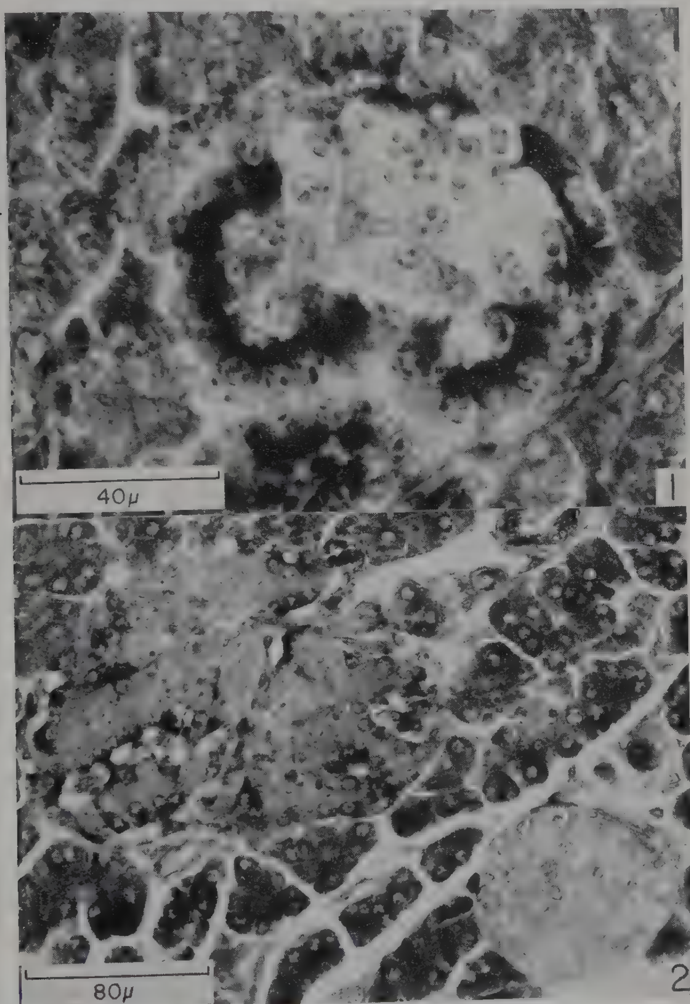
alpha cells, while still primarily central, are either more eccentrically arranged or are in cords among the beta cells. *Dipodomys merriami* most closely approaches the condition in *D. deserti*. Central and partly scattered cords of alpha cells among the beta cells characterize the examined specimens of *Perognathus* (species: *inornatus, parvus, penicillatus*). The structure of the islets in *Heteromys* and *Liomys,* the remaining genera of Heteromyidae, is not known, nor has it been previously described in other members of the Geomyoidea. However, a single specimen of *Thomomys bottae* fixed in 10 per cent neutral buffered formalin shows scattered alpha cells near the centers of the islets. A specimen of *Ammospermophilus leucurus,* a desert sciurid, shows a similar condition.

In some carnivores it has been shown that the islets of the ventral part of the pancreas lack alpha cells and the dorsal and retro-splenic portion has abundant alpha cells along with the beta cells (Bencosme

TABLE I.—Percentages of alpha cells (1000 chromophil cells counted/-animal) in islets of desert rodents stained with Halmi's aldehyde fuchsin technique after fixation in Bouin's fluid (n = number of specimens; x = mean).

Name Locality	n	x	range
Heteromyidae			
Microdipodops sp. Mono Lake, California	3	32.0	29-38
Dipodomys merriami Fletcher, Nev.	3	41.3	37-45
D. panamintinus Fletcher, Nev.	1	34.0	
D. heermanni Pinnacles, Calif.	1	25.0	
D. deserti Trona and Keeler, Calif.	4	24.5	16-33
D. ordi Bodie, Calif.; Fletcher, Nev.	2	22.5	20-25
D. nitratoides McKittrick, Calif.	1	22.5	
D. microps Fletcher, Nev.	3	17.7	15-22
Perognathus parvus Lee Vining, Calif.	1	41.0	
P. penicillatus Borrego, Calif.	3	27.0	23-32
P. inornatus McKittrick, Calif.	1	25.0	
Sciuridae			
Ammospermophilus leucurus Inyokern, Calif.	1	28.0	

and Liepa, 1955). The possibility of regional differences in the relative numbers of these cells in the heteromyid pancreas was checked in six specimens by means of counts of islet cells in blocks of tissue from retro-splenic and juxta-intestinal sites. In *Dipodomys deserti* (1 specimen) and *Perognathus penicillatus* (3 specimens) the alpha: beta cell ratio is about the same in the two areas. In *D. nitratoides*



Figs. 1-2.—Pancreatic islets of *Dipodomys* after fixation in Bouins's fluid and staining with aldehyde fuchsin. 1.—Small islet with peripheral beta cells (dark) and central alpha cells; *D. nitratoides* ♀, McKittrick, California. 2.—Medium-sized islet with eccentric mass of alpha cells, upper left, and a ganglion, lower right; *D. deserti* ♂, Trona, California.

and *P. inornatus* on the other hand the retro-splenic pancreas had a higher alpha cell ratio (27 versus 18 per cent, 32 vs. 18 per cent respectively). Since these differences were found in but single animals of each species, their significance may be questioned.

The percentage of alpha cells in comparison with beta cells in the heteromyid islets appears to be high (Table I). And there seem to be species differences, and perhaps parallel evolutionary trends, within the genera *Dipodomys* and *Perognathus*. The antelope ground squirrel (*Ammospermophilus*) also has a high percentage of alpha cells.

Other distinctive characteristics of the heteromyid islets include several features whose significance is difficult to evaluate at this time. A relatively large number of ganglia in the heteromyid pancreas in relation to that of other rodents is one such characteristic (Fig. 2). Cytologically the islets of captive as well as some feral heteromyids are frequently notable for the extreme size of the nucleoli in the chromophils (Figs. 1 and 2). The nucleolar diameters not uncommonly equal or exceed one-half of the nuclear diameters. Inasmuch as nucleolar size has been correlated with the activity of islet cells (Kracht, 1958), heteromyid islets appear to provide unusually interesting material for studies of nucleolar variations and their meaning. Mitoses were seen in two areas of the islets, most commonly along the periphery, and sometimes in the boundary between alpha and beta cellular zones. None of the mitotic cells contained beta granules, and it was uncertain whether a few of them contained alpha granules.

Discussion

Among the rodents previously studied the alpha cells are either primarily scattered within the islets (*Cricetus auratus, Cavia cobaya, Sciurus carolinensis, Tamiasciurus hudsonicus*) or are peripheral (*Mus musculus, Rattus norvegicus, Peromyscus* sp., *Pitymys* sp., *Dicrostonyx groenlandicus*) (Lane, 1907; Thomas, 1937; Hard, 1944; Jewell, 1951; Quay, unpublished observations). Within the Heteromyidae, and perhaps in a considerable number of the Geomyoidea, the alpha cells tend to be central in position, and most markedly so as far as our material is concerned in *Microdipodops*. The fact that these are alpha cells rests on the solubility of their cytoplasmic granules and their staining reactions. In *Ammospermophilus* a more central location of the alpha cells is true in this desert species in contrast to the above previously studied sciurids. Central location for the alpha cells has been noted also in the horse (Gomori, 1939). However, relatively few mammalian taxa have been studied in this regard. Nevertheless the trend within the heteromyids and what little we know from other mammals supports a general correlation between central position of alpha cells and life in an arid environment. The physiological meaning of this, if any, is obscure and may be related possibly to the times of differentiation of the cell types in the fetal or young animal. In the rat (*Rattus*) beta cells differentiate during embryonic develop-

ment and the alpha cells are not recognizable until the second day of postnatal life (Hard, 1944).

The alpha:beta cell ratio is lower in other rodents (*Cricetus auratus* — 19.1 per cent; *Cavia cobaya* — 19.9-22.2 per cent; *Rattus norvegicus* — 5-18 per cent; *Dicrostonyx groenlandicus* — 5.6-16.5 per cent; Müller, 1959; Quay, unpublished) than in the desert species studied here. Among other mammals a high percentage or ratio of alpha cells has been found in the horse (Gomori, 1939) and the few marine forms studied, "seal" (Thomas, 1937) and beluga (*Delphinapterus*) (Quay, 1957). Although the physiological significance of these variations in mammalian islets has remained unstudied and obscure, in some lower tetrapods a relatively high percentage of alpha cells appears to be associated with higher blood sugar levels and greater resistance to insulin (Miller and Wurster, 1959). The alpha and beta cells of the mammalian islets are believed by most investigators to be the sources respectively of the hormones, glucagon (Foa, Galansino and Pozza, 1957) and insulin (Barnett, Marshall and Seligman, 1955), although some controversy persists in regard to glucagon. There appears to be an interrelationship between glucagon and insulin in their actions (De Bodo and Altszuler, 1958). And a hyperglycemic-glycogenolytic activity is usually ascribed to glucagon, but other effects have been noted, including modification of blood cholesterol level (Caren and Carbo, 1956) and blood non-protein nitrogen level (Bencosme, Toledo and Craston, 1959). It has been pointed out, particularly by the Schmidt-Nielsens (1952), that some kangaroo rats (*Dipodomys*) do not need drinking water or moist food and that their production and conservation of metabolic water may be greater from carbohydrate and fatty rather than protein food materials. This information with the islet specializations noted above suggests the value of comparative studies of the significance of the islets and their hormones to the metabolic activities of both young and adult desert rodents.

SUMMARY

The microscopic anatomy and cytology of the pancreatic islets in four genera of North American desert rodents (*Dipodomys, Microdipodops,* and *Perognathus* of the Heteromyidae, and *Ammospermophilus* of the Sciuridae) were studied after treatments with seven fixatives and five staining techniques. The following characteristics appear to distinguish the islets of some or all of the desert species examined: (1) central clumping of alpha cells, (2) relatively high alpha:beta cell ratio, and (3) preservation and staining of beta cell granules by aldehyde fuchsin following Helly's-formalin and formalin-isopropanol fixatives. Parallel trends within *Dipodomys* and *Perognathus* occur with respect to at least the first two of these characteristics. Other microscopic features and the possible physiological significance of the findings are discussed.

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Studies on the Larval Morphology of Ascaris laevis Leidy, 1856*

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Adult nematodes of the genus *Ascaris* Linn., 1758 are seldom found in rodents. Four species are listed by Hall (1916): *A. castoris* Rudolphi, 1809, from *Castor fiber; A. laevis* Leidy, 1856 from *Marmota (Arctomys) monax; A. pigmentata* von Linstow, 1897, from *Marmota marmota; Ascaris* sp., reported by Parona in 1909, from *Mus minutoides. Ascaris castoris* and *Ascaris* sp. were inadequately described and *A. laevis* was recently redescribed by Tiner (1951) from specimens obtained from Pennsylvanian and Alaskan woodchucks. Tiner also considered worms identified as *A. columnaris* Leidy, 1856 by Linsdale to be "a variant of *A. laevis*." Because of certain morphological characteristics possessed by *A. pigmentata* which resemble those of the subfamily Anisakinae Railliet and Henry, 1912, Hall felt that this species belonged in another genus. He further suggested that perhaps *Ascaris* sp. and *A. castoris* were erroneously placed. *Ascaris joffi,* from *Citellus pygmaerus* and *A. tarbagan,* from *Marmota sibirica* were described by Schultz (1931). *Ascaris lumbricoides,* genotype, is primarily a parasite of humans and pigs; however, there have been several reports of the accidental occurrence of the species in sciurids (*Sciurus niger,* by Rausch and Tiner, 1948 and by Thomas (cited by Brown and Yeager, 1945); *S. indicus* listed by Baylis, 1939) and murids (*Ondatra zibethica* by Tiner and Chin, 1948).

Specimens of *A. laevis* were collected from several ground squirrels, *Citellus undulatus,* on St. Lawrence Island, Alaska by Dr. L. J. Thomas and the writer. The range of infection was 2 to 4 worms per animal. Because of the infrequent occurrence of members of the genus in rodents and the lack of adequate information relative to the life history of such forms, experimental studies with the species were undertaken. Pathology in experimentally infected hosts due to *A. laevis* was reported by the writer (1959) and a paper on the "tracheal-migration" of the species is in press. The present study on larval morphology is primarily based upon material observed in and recovered from experimentally infected hosts (*Citellus tridecemlineatus, C. franklini,* and *Marmota monax*).

The Egg

The organization of mature unsegmented ova of *A. laevis* apparently is similar to those of *A. lumbricoides* as described by Martin

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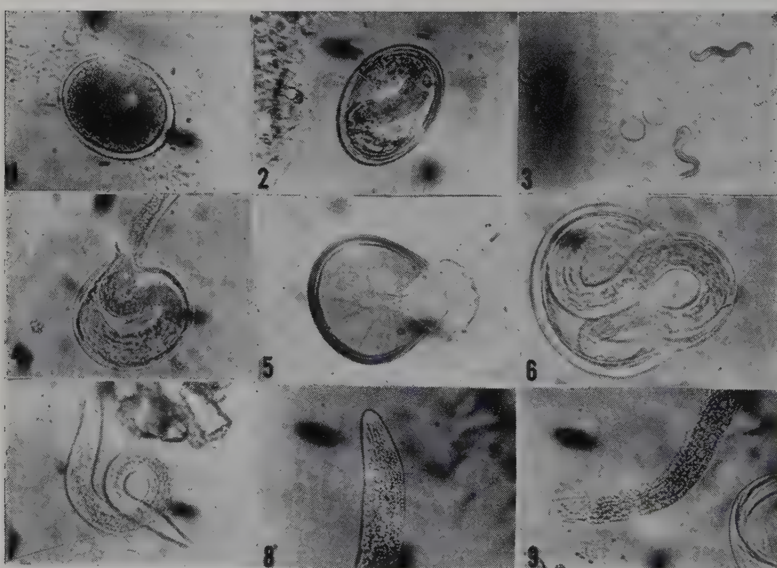
(1926), Roberts (1934), and Rodgers (1956). The fertilized egg of *A. laevis* is oval in outline with a semi-transparent shell about 3 to 5 μ thick. The cytoplasm appears to be composed of a large number of granules within a colorless matrix. The nucleus (Fig. 1) is more distinct in fertilized eggs than in non-fertilized ones.

The size of *A. laevis* eggs as given by Tiner (1951) ranged from 0.067 - 0.069 mm in length and from 0.051 - 0.054 mm in width. Of 50 eggs measured by the writer, the length ranged from 0.06 - 0.08 mm, with an average of 0.075 mm, and the width from 0.05 - 0.07 mm, with an average of 0.058 mm.

Embryonation of *A. laevis* eggs was observed to be of typical ascarid development. When teased from the uteri of a mature female worm and incubated at room temperature (25-30° C.) in distilled water, the eggs attained the two-celled stage in less than 24 hours, the morula stage in 4 to 6 days and in 8 to 12 days motile vermiform embryos were seen within the shells. The infective stage was reached by the 17th day (Fig. 2).

By either observing the eggs in the process of being de-shelled in a NaOH-NaC1 solution (Elliot, 1954) or by applying slight mechanical pressure to the cover-glass, embryos of *Ascaris laevis* could be



Figs. 1-9.—Photomicrographs showing hatching of second stage larvae of *Ascaris laevis*. 1. A fertilized egg. 2. An embryonated egg. 3-4. Hatched and hatching larvae. 5. Ruptured vitelline membrane left behind in the stained egg-shell. 6. Escaping larva enclosed within the vitelline membrane. 7. Recently hatched larva. 8. Anterior end of larva showing hyaline granules. 9. Posterior part of larva showing hyaline granules. (Figs. 1, 2, 4, and 7, ×800; Fig. 3, ×180; Figs. 6, 8, and 9, ×1680.)

released from the egg. Apparently, the egg contains no predetermined place for hatching to occur and rupture seems to take place at a point of least resistance. As the shell splits in a V-shaped manner a portion of the vitelline membrane may extrude through the opening and the embryo escapes after having ruptured the thin membrane at this point. The entire vitelline membrane with the embryo contained in it may escape from the egg, with the young worm becoming completely free of the membrane. Generally, the vitelline membrane is left behind (Fig. 5) when the larva escapes from the shell. Escape appears to be accomplished by the hyper-activity of the organism which apparently produces internal mechanical pressure upon the outer cell wall. The so-called "boring-tooth" described by several investigators for *A. lumbricoides* was not observed for *A. laevis*. The manner in which the worm leaves the egg is not consistent, it may leave tail-first (Fig. 3 and 4), head-first, or even in a U-shaped manner with the mid-body region being freed first (Fig. 6). The moulted cuticle either may be left within the egg-shell or be retained by the larva (Fig. 16). Worms of older egg-cultures appear to leave their shedded cuticles behind more frequently than those from younger ones.

Description of Ecdysis and Larval Stages

ecdysis

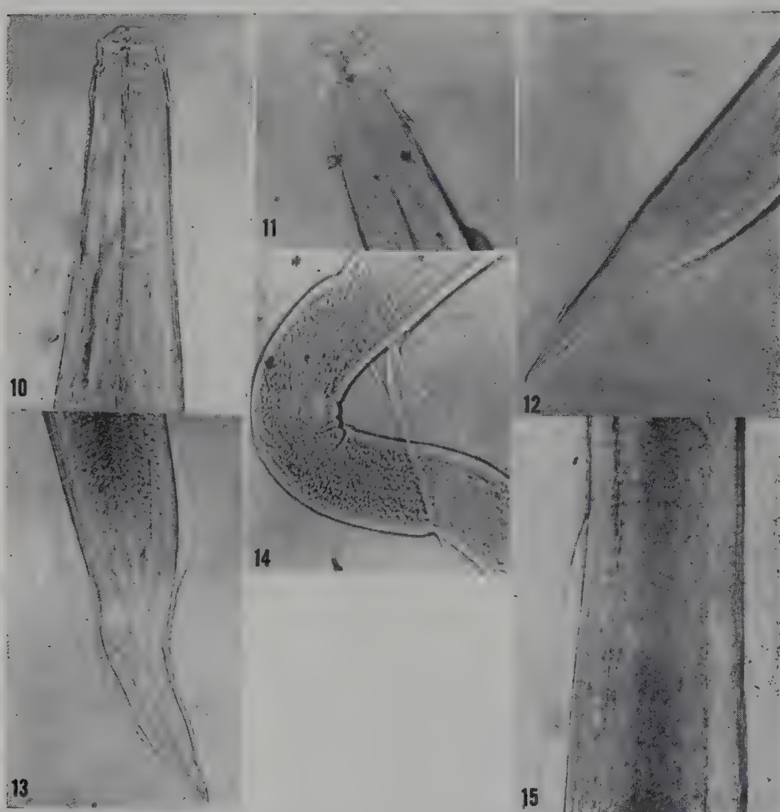
There is considerable inconsistency between nematode groups in the times and patterns in which they moult. Such differences apparently exist within a given species. Much of the knowledge accumulated on this phenomenon has been obtained by the use of chemical materials. Chance observation of a moulting parasitic larva is not common, and frequently the process is neither readily recognized nor understood by the inexperienced investigator. During these studies, the writer was fortunate to have observed ecdysis in several larval stages.

Ascaris laevis has five larval stages, each of which except the first is preceded by ecdysis and a growth phase. The first moult within the egg has been mentioned, all others are in the viscera. The second moult takes place within the liver 10 to 12 days after the infection. Casts of discarded cuticles may be recovered from the organ at this time. Third stage larvae remains for a prolonged period of time within the liver and grow slightly. A description of a second stage larva in the process of moulting was recorded as follows:

> Worm is retracted. The unsheath cuticle is fitted loosely about the worm, although it is still attached at intervals along most of the body. The cuticle is greatly inflated at the tail-region and the worm is having difficulty in freeing the tail due to the attachment of the cuticle to the rectum. In the labial region, the loosened sheath is pulled far anteriorly but the lining of the esophagus is still attached to the mouth. The worm lashes about freely within the sheath apparently trying to free the mouth attachment.

The third ecdysis probably takes place either while the organism is enroute to the lungs or shortly after it gets there (between 34 to

73 days after the infection). In a few cases this moult may occur in the liver. When early fourth stage larvae (worms which recently moulted) are found in the lungs, late-fourth stage larvae (worms which will soon moult) may be found in the intestine. Ecdysis by fourth stage larvae also was observed and a composite description of the process is presented. The cuticular sheath is duplicated and soon becomes inflated in a blister-like manner about most the worm (Figs. 10, 12 and 15). Labial, esophageal, and tail papillae become greatly modified — the lips become bluntly rounded, but the labial papillae interrupt their



Figs. 10-15.—Photomicrographs showing process of ecdysis by late fourth stage larvae of *Ascaris laevis*. 10. Anterior end of worm. Cuticle has been pulled in to form a hood-like structure about the lips; 11. Anterior end of worm. Cuticle was extended in advance of the labial region but the esophageal lining is still attached; 12-13. Posterior end of worms. Tail regions were distorted and the cuticle inflated to resemble caudal alae. 14. Region of vulva. Worm tried to exsheath through a longitudinal split in old cuticle. 15. Mid-body region of worm. Showed inflation of cuticle. (Figs. 10, 12, 13, 14, and 15, ×200; Fig. 11, ×1000.)

contour; the esophagus appears more slender and somewhat extended; the tail becomes greatly attenuated posteriorly (Figs. 12 and 13). The loosened cuticle about the labial region may be pulled in by the worm to form a hood-like structure about the lips (Fig. 10), or may extend far in advance of the lips, although maintaining attachment to the esophageal lining (Fig. 11). The sheath about the tail is greatly inflated to resemble large caudal alae, but attachment to the rectal lining persists for some time. Eventually, the sheath ruptures longitudinally in the region of the second quarter of the body to free this portion of the worm and ultimately allows complete unsheathing (Fig. 14).

LARVAL STAGES

Second Stage Larvae.—A recently hatched larva is long, slender, and encased in a close-fitting delicate cuticular membrane, which is not yet striated (Figs. 7, 16). The anterior end of the worm is bluntly rounded (Fig. 8) and the posterior end (Fig. 9) gradually tapers. The body is completely filled with hyaline granules[1] which are somewhat more abundant in the region of the intestine (Fig. 16). The lip region is conspicuous, being set-off slightly from the rest of the body. The lips themselves, however, are not yet formed but the cuticle in the labial region is fitted into a three-parted assemblage. The indistinct esophagus, not sharply delimited from the intestine, is slightly rhabditiform with its greatest width near the esophageal-intestinal juncture. The excretory pore can be seen but the nerve ring is not yet discernible. The heavy granulation about the esophagus (Fig. 8) prevents further visibility of structures within this region. The genital primordium is not discernible. The anus, situated ventrally, is recognized by an oblique slit in the cuticle near the posterior end of the body. Of 50 worms measured from five egg-cultures, the length ranged from 0.14 - 0.32 mm, with an average of 0.25 mm. The maximum width is more or less uniform and averaged, 0.02 mm. The length of the esophagus ranges from 0.07 - 0.09 mm, with an average of 0.08 mm. The excretory pore is 0.04 - 0.05 mm from the anterior end, with an average of 0.04 mm. The indistinct anus is 0.02 - 0.03 mm from the posterior end, with an average of 0.02 mm.

Second stage larvae in the liver of an experimental host shows slight modification in morphology three days after parasitizing with embryonated eggs. The body of such larva is long and slender (Fig. 17). A distinct body space can be seen. The labial region forms a

[1] Chitwood (1950) classified the intestinal cell inclusions as either food reserves or waste products. The hyaline granules, considered to be food reserves, in the intestine of ascarids were referred to as "zymogen granules" and were considered to be associated with the synthesis and decomposition of glycogen. Clark (1955) identified the cell inclusions (considered to be waste products), strongylin, from *Strongylus* spp. and rhabditin, from *Rhabditis strongyloides* as beta zinc sulfide and xanthine, respectively. L. J. Thomas (personal communication) feels that the hyaline granules in larvae of *A. laevis* may be one of the two products identified by Clark.

knob-like structure which is clearly delimited from the rest of the body. Hyaline granules are distributed throughout the length of the worm but are more concentrated in the region of the intestine than in the esophageal and tail areas. The esophagus is short and muscular but still somewhat concealed by granules. The nerve ring is not discernible. The excretory pore is prominent. Measurement of ten "3-day-old larvae" show a length ranging from 0.28 - 0.39 mm, with an average of 0.36; a width of 0.02 mm; an esophagus length from 0.08 - 0.10 mm, with an average of 0.09 mm; and a distance of the anus from the posterior end from 0.02 - 0.03, with an average of 0.02 mm.

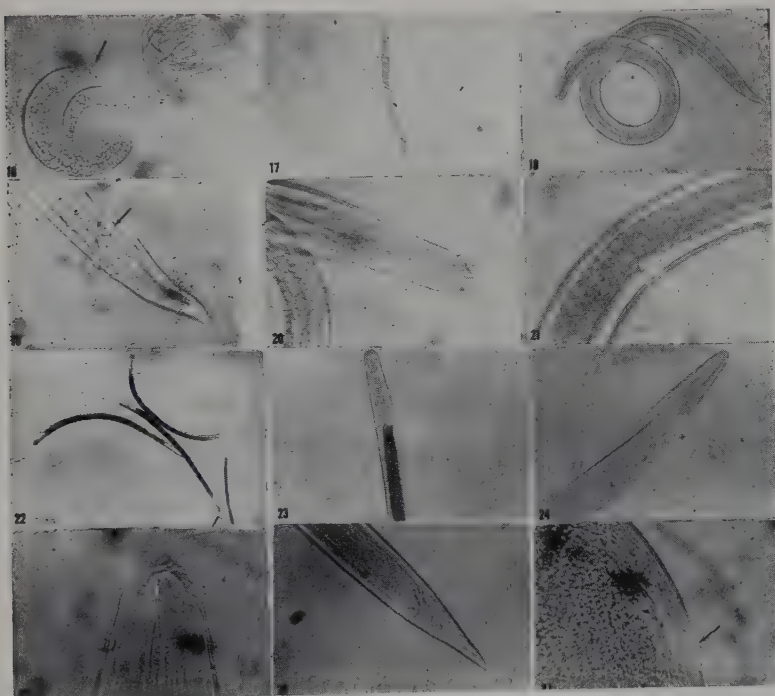
By the 17th day, most larvae increased in length. The lengths of 30 worms studied ranges from 0.37 - 0.87 mm, with an average of 0.63 mm. The body cuticle of such a larva contains vague striations. The labial region begins to show the lip pattern of the adult. The esophagus is clearly visible and has lengthened proportionately with the body. The nerve ring is not distinct but can be distinguished. The excretory pore, duct and cell are visible; the latter is situated near the esophagus. The prominent excretory columns occupy much of the body space. The intestine still has more granules than the tail and esophageal regions. The anus is discernible and the tail tapers sharply.

Third Stage Larvae.—Study of about 200 third stage larvae (Fig. 18) showed that generally they can be distinguished from second stage larvae by the following characteristics: (1) the body is longer and more cylindrical; (2) the cuticle is distinctly striated; (3) narrow lateral alae extend the length of the body; (4) the lips are slightly more defined and contain papillae which are vaguely discerned (Fig. 20); (5) the filariform esophagus, nerve ring, and excretory duct, are prominent; (6) the genital primordium can be seen (Fig. 21); (7) gland-like cervical cells (possibly arcade cells) are present about the anterior esophageal area; (8) there is a reduction in the number of granules, especially about the esophageal and tail regions; (9) the anal lips, rectum and rectal glands are visible (Fig. 19); (10) the hexagonal-shaped intestinal cells, each of which contains a basophilic nucleus, can be seen.

Sizes of third stage larvae show a wide variation. The length ranges from 0.09 - 1.40 mm, with an average of 1.04 mm; the width from 0.03 - 0.06, with an average of 0.05 mm; the esophagus, which in some specimens may still be partially concealed by hyaline granules, has a length which averaged about 0.02 mm; the nerve ring, discernible in most larvae despite some granulation in the area, is located between 0.07 - 0.08 mm from the anterior end of the esophagus, with an average of 0.07 mm; the excretory pore is 0.10 - 0.11 mm from the anterior end of the body, with an average of 0.10 mm; the anus, which leads inward to a cuticularized rectum, is situated 0.05 - 0.07 mm from the tip of the tail, with an average of 0.06 mm. The long straight intestine which occupies most of the body is filled with yellowish-brown particles of ingesta, which makes this portion of the body

appear darker in contrast with the esophageal and tail regions. The genital primordium is ventral and in the third quarter of the body. The excretory columns extend posteriad throughout the body. The conical tail curves dorsally.

Fourth Stage Larvae.—Study of 15 early fourth stage larvae revealed that differences between these worms and late third stage ones are not apparent without detailed morphological comparisons. Size is not a criterion since there may be some over-lapping. The obvious characteristics which distinguish early fourth stage larvae are: (1) the



Figs. 16-27.—Photomicrographs of second, third, early and late fourth stage larvae of *Ascaris laevis*. 16. Recently hatched second stage larva. Moulted cuticle can still be seen at anterior end of worm. 17. Second stage larva collected from liver three days after experimental feeding. 18. Third stage larva. 19. Posterior end of third stage larva showing rectal glands. 20. Anterior end of third stage larva showing incompletely developed lips. 21. Body region of third stage larva showing genital primordium. 22. Several early fourth stage larvae collected from lungs. 23. Anterior end of early fourth stage larva showing indistinct esophagus, excretory columns, and portion of intestine. 24. Anterior end of late fourth stage larva with lips set-off from body. 25. Labial region of late fourth stage larva showing lips and some papillae and muscular esophagus. 26. Posterior end of late fourth stage female showing pointed tail. 27. Portion of body of late fourth stage larva showing rudimentary vulva. (Figs. 16, 19, 20, 21, 25, and 27, ×1000; Figs. 17, 23, 24, and 26, ×200; Fig. 18, ×800; Fig. 22, ×59.)

possession of cuticular annulations; (2) the almost complete absence of hyaline granules in the esophageal and tail regions (Figs. 22, 23); (3) the greater amount of space occupied by the excretory columns; (4) the vagueness of the intestinal cells; (5) the more completely developed lips with their prominent labial papillae; (6) the recognition of sex (the male, by its papillated tail; the female, by its rudimentary vulva). Generally, the esophagus, nerve ring, excretory pore, excretory duct, and excretory cell is more pronounced than in earlier stages since there are fewer granules present to obscure observation of these structures. Early fourth stage larvae are more often found in the lungs than in the intestine.

The size of early fourth stage larvae are as follows: length, 1.40 - 2.20 mm, with an average of 1.70 mm; maximum width, 0.05 - 0.08 mm; length of esophagus, 0.10 - 0.27 mm, with an average of 0.23 mm; nerve ring from the anterior end, 0.05 - 0.12 mm, with an average of 0.09 mm; excretory pore from the anterior end, 0.07 - 0.16 mm, with an average of 0.12 mm; distance of anus from posterior end, 0.06 - 0.08 mm, with an average of 0.07 mm.

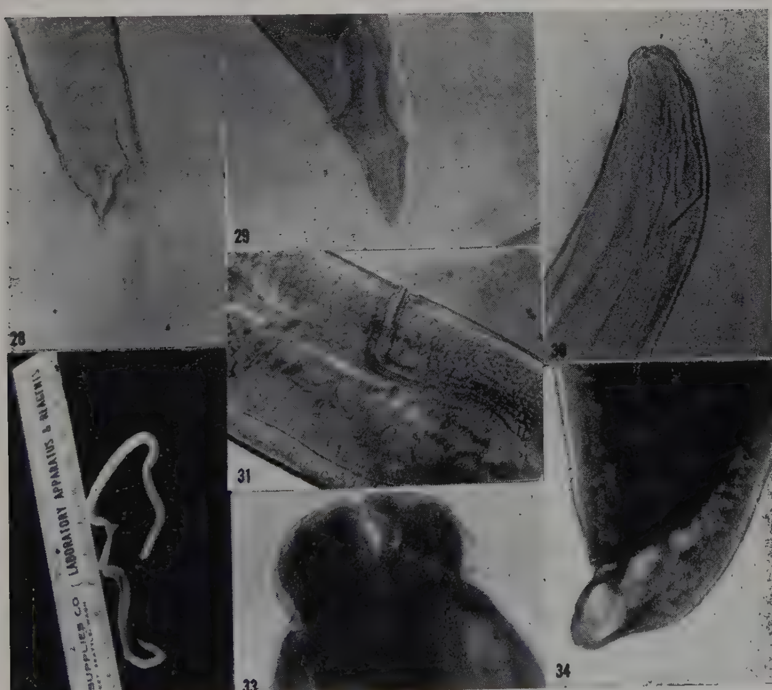
Late fourth stage larvae show considerable variation and are readily distinguished from early fourth stage worms. These larvae are always found in the small intestine. They may be characterized by (1) a large size, (2) lips which are set-off from the body and which nearly resemble those of the adult (Figs. 24, 25), (3) a strongly muscularized esophagus, (4) the absence of hyaline granules, and (5) the greater advancement of sex differences — the tail of the male is bluntly rounded with prominent papillae; the female has a rudimentary vulva (Fig. 27) and in some of the larger specimens genital tubules are present. The tail of the female is sharply tapered (Fig. 26).

The size of late fourth stage larvae varies considerably, some measurements are as follows: total length, 2.80 - 16.40 mm; maximum width, 0.09 - 0.34 mm; length of esophagus from the anterior end, 0.39 - 0.97 mm; anus from the posterior end, 0.09 - 0.27 mm.

Fifth Stage Larvae.—Advanced development of reproductive organs, prominent lips being less in diameter than the rest of the body, the close proximity of cuticular annulations, a strongly cuticularized and muscular body, and the more anterior level of the nerve ring and excretory pore primarily serve to distinguish these worms from those of the earlier stage. Size is not always a reliable character since there may be some over-lapping with worms of the late fourth stage. The following description is based upon a composite study of six worms recovered from ground squirrels and woodchucks.

Male: The stout cuticle is distinctly striated with numerous annulations (Figs. 28, 30) which appear prominent in the anterior half of the worm and in the tail region. The body musculature is distinctly polymyarian. Three cuticularized lips, sharply set-off from the body and each possessing well-defined papillae, are present. The esophagus is highly muscularized (Fig. 30) with radially directed

fibers which present a transversely striated appearance when the worm is studied morphologically. The esophagus is wide near the labial region but tapers posteriorly for a short distance before assuming a club-shaped appearance. The greatest diameter of the esophagus is at the region of the bulbus. The nerve ring is vague in outline but its location is recognizable by groups of sensory ganglia concentrated about 0.32 mm from the anterior end of the esophagus. The ventrally situated excretory pore opens into the cuticle from an obliquely directly canal which is concealed posteriorly by muscle cells, nerve ganglia, and mesenteries. A wide intestinal lumen extends a slightly irregular course from the esophagus to the cloaca. Within the intestine are large brownish particles of ingesta which presents a granular appearance to the organ. The anus, approximately 0.30 mm from the posterior end, is almost ventral and leads inward from an obliquely directed sub-triangular rectum to the cloaca (Fig. 28). Rectal glands are not as prominent as in the two earlier stages of the parasite. Dor-



Figs. 28-35.—Photomicrographs and photographs of immature and mature adults of *Ascaris laevis*. 28. Posterior end of immature male (lateral view). 30. Anterior end of immature adult showing prominent lips and a strong muscularized esophagus, and excretory nucleus. 31. Portion of body showing the vulvular region of an immature adult female (lateral view). 32. Mature adult. 33. Lips of mature adult (lateral view). 34. Posterior end of mature female (dorso-lateral view). (Figs. 28, 29, 30, 32, 33, and 34, ×200; Fig. 31, ×1000.)

sally and immediately anterior to the anal opening are two short spicules lying in spicular pouches which unite to become continuous with the cloaca (Fig. 29). Details of the secondary reproductive structures cannot be discerned with accuracy. The tail region posterior to the anus contains tactile papillae which appear slightly stalked. On the blunt part of the tail are three pairs of tandem papillae. A fifth pair of sensory structures is apparently adanal in position. Preanal papillae, less prominent and perhaps a little smaller than ad- or postanal papillae, extend irregularly cephalad. Forty-seven pairs of papillae can be counted with certainty.

Female: The labial and esophageal regions are similar to those of the fifth stage male. The tail region is without papillae but possesses irregularly distributed phasmids (chemo-receptors). The tail is more bluntly rounded than that of male specimens. The vulva is ventral and located about 3.83 mm from the anterior end of the body. It leads inward to a short muscular cuticularized vagina (Fig. 31) which, for a distance of about 0.23 mm, extends slightly oblique toward the tail. Subsequently, the vagina bends posteriad at a right angle and bifurcates from the vaginal trunk to differentiate into thin-walled, slightly muscularized uteri which extend caudally for about 1.50 mm. At this distance the distal part of each uterus gives rise to a long tube-like ovary which coils extensively in a posteriad direction.

Size variation of fifth stage female larvae is as follows: total length, 24.70 - 32.40 mm; maximum width, 0.42 - 0.59 mm; length of esophagus, 1.77 - 3.75 mm; nerve ring from anterior end, 0.28 - 0.35 mm; excretory pore from anterior end, 0.29 - 0.37 mm; vulva from anterior end, 3.76 - 3.91 mm; anus from posterior end, 0.30 - 0.33 mm.

SPECIAL FEATURES OF THE ADULT AND SYNONYMY

With few minor variations the morphology of mature adult specimens of *A. laevis* as studied by the writer fits the redescription of the species as given by Tiner (1951). Two additional features which may be of diagnostic value are discussed below.

THE LIPS

Characteristic of the genus *Ascaris* is the presence of three cuticularized lips, one dorsal and two ventro-lateral (Figs. 33 and 35). The greatest size of the former in an average-sized adult of *A. laevis* (Fig. 32) measures 0.35 mm in width and 0.25 mm in length. The latter lips are about equal measuring 0.29 mm wide and 0.21 mm long. The morphology of the lips are somewhat similar to those of *A. devosi* as described by Sprent (1952). The pulp of each lip has two components, an apical part containing the internal papillae and the basal part containing the external papillae and phasmids. Two sub-oval dark areas comprise the former part, each of which is approximately 0.71 mm long and containing a deep groove extending inward from the mouth. A small papilla is situated at the base of

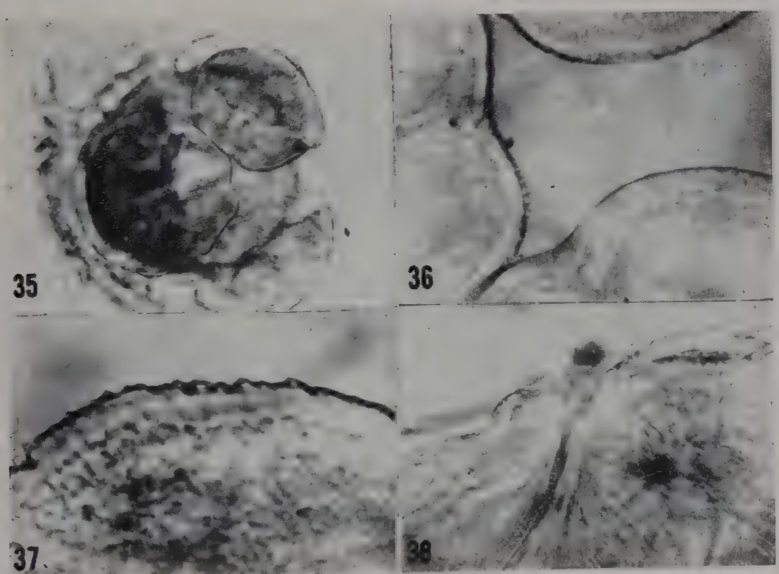
each groove. The pulp of the latter part resembles the musculature of the anterior esophagus. The basal part of each lip contains two pairs of external cuticularized papillae on its outer surface. The papillae on the dorsal lip appear larger than those on the ventrolateral lips. Denticulated processes are irregularly distributed over the oral surface of each lip (Figs. 36 and 37). Those along the inner lip surface are somewhat triangular (Fig. 36) and attain a height of about 0.52 mm. Toward the outer lip surface the denticles gradually assume a dome shape and become smaller until they can be recognized no longer (Fig. 37).

THE ANAL REGION

In the pre-and post-anal areas of the male are cuticularized bosses which are irregularly distributed for an equal distance of about 0.04 mm. These cuticular roughenings end abruptly at the anal opening (Fig. 38). It is of interest that this characteristic also was described by Sprent for the ascarid in the fisher and marten, *A. devosi.*

SYNONYMY

A comparative examination of the description and illustrations of *Ascaris tarbagan* described by Schultz (1931) from a Siberian wood-



Figs. 35-38.—Photomicrographs showing views of lips and anal region of adult worms. 35. En-face view of lips. 36. En-face view of lips showing denticles. 37. En-face view of portion of dorsal lip showing shape and distribution of denticles. 38. Lateral view of cloaca showing peri-anal roughenings. (Fig. 35, ×200; Fig. 36, ×1,000; Figs. 37, and 38, ×1,680.)

chuck (*Marmota siberica*) and later reported from an Alaskan woodchuck (*Monax monax ochracea* Swarth) by Phillip (1938) reveals that this species is co-specific with *A. laevis* as redescribed by Tiner and as studied by the present writer (Table I). It is therefore suggested that *A. tarbagan* be considered a synonym of *A. laevis*. It is conceivable that *A. laevis* (syn. *A. tarbagan*) in ground squirrels of St. Lawrence Island, Alaska is of Siberian origin, since few mammals are indigenous to the island. *C. undulatus,* the host from which the writer's material was originally collected, is widely distributed in Asia. A detail discussion of the occurrence of this ground squirrel in Siberia is given by Ognev (1947).

TABLE I.—Some morphological comparisons in millimeters between *Ascaris laevis* and *A. tarbagan*

Characters	*A. laevis* (Tiner, 1951)	*A. tarbagan* (Schultz, 1931)	*A. laevis* (present study)
	Females		
Total length	80-100; 135*	92-169	78-139
Maximum width	2.40-2.60	1.73-2.60	1.70-2.50
Esophagus			
length	4.50-5.10	3.48-4.64	4.20-5.10
width	0.59-0.71	0.91	0.42-0.62
Nerve ring from anterior end	0.75-0.90	—	0.52-0.74
Excretory pore from anterior end	1.12-1.16	0.83-0.88	0.78-0.98
Vulva from anterior end	20-28	17-36	19-32
Anus from posterior end	0.58-0.83	—	0.57-0.76
Egg-size			
length	0.07	0.07-0.08	0.06-0.08
width	0.05	0.07	0.05-0.07
	Males		
Total length	30-48; 72*	57-65	42
Maximum width	1.2-1.8	1.16-1.37	0.94
Esophagus			
length	2.45-3.64	3.30-3.40	3.89
width	0.32-0.50	0.43-0.50	0.32
Nerve ring from anterior end	0.44-0.55	0.66-0.68	0.40
Excretory pore from anterior end	0.63-0.75	0.71-0.79	0.57
Anus from posterior end	0.38-0.41	0.43-0.46	0.41
Spicule length	0.36-0.55; 0.41-0.54*	0.38-0.56	0.36

* Measurements obtained from *C. beecheyi* specimens, which Tiner considered to be a "variant" of *A. laevis*.

SUMMARY

The morphology of the larval stages of *Ascaris laevis* Leidy has been described, as well as certain anatomical features of the adult worm. Some observations on the development and hatching of the eggs of the parasite and ecdysis by several larval stages have been discussed. *Ascaris tarbagan,* from *Marmota siberica* was considered a synonym of *A. laevis.*

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Observations on the Offshore Benthic Flora in the Gulf of Mexico off Pinellas County, Florida[1]

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The Floridian Plateau is that projection of North America which separates the deep water of the Atlantic Ocean from the deep water of the Gulf of Mexico (Vaughan, 1910). According to Cooke (1945) the Plateau includes both the State of Florida and an equally great or greater area that lies submerged in water less than 50 fathoms deep. Gunter (1929) called this submerged portion the Florida Shelf. The shelf width in the vicinity of Pinellas County is approximately 105 miles. The offshore slope is gradual in certain areas and at a distance of 40 miles offshore in the Gulf of Mexico the bottom may be under approximately 100 feet of water.

The present report contains a discussion of the benthic algal flora collected 9 - 20 miles offshore at depths from 35 - 60 feet. It is not known if attached algae occur to the offshore edge of the shelf, however, the fact that they are found so far offshore is significant. It is probable that algal growth will be found at distances further offshore and in water deeper than investigated at the present.

Several papers contain information on the marine algae of the Gulf coast of Florida. These are: Taylor (1928, 1936, 1954, 1954a), Nielsen and Madsen (1949, 1949a), Madsen and Nielsen (1950), Humm (1953), and Earle (1956). Humm (1956) listed algal records from inshore and offshore waters in an unpublished general checklist of the St. Georges Sound-Apalachee Bay region in northwest Florida. Excepting Humm (1956) and Taylor (1928), all the other papers cited here concern work confined to bay and close-shore waters.

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[2] Contribution No. 43.

METHODS AND MATERIALS

The reef areas were located with the aid of a fathometer. SCUBA-type diving equipment was used in collecting, and thus we believe that adequate sampling was made at most stations. The first few collections are doubtfully representative as the perfection of the use of the diving gear was of prime concern. Algae collected by the junior author were incidental to the collection of fishes, but usually a concerted effort was made to obtain a thorough sample. The importance of the use of SCUBA equipment cannot be overemphasized, for it represents the contrast between visual observation and the aimless wanderings of the collecting dredge. Collection periods of one-half hour to two hours were allowed with the use of the diving equipment.

A small chipping hammer was used at times to aid in the removal of the more firmly attached plants. While in the water the collected algae were retained in a small-mesh nylon bag. Preservation was made in ten per cent formalin upon return to the boat.

Eight collections were made in 35 - 40 feet depths and 12 in 45 - 60 feet depths during a one year period. The collections have been lumped into these two depth ranges, owing to the assemblage of plants found in each. It is possible that further study will reveal a "continuum" of plant distribution from shallower depths to the deeper depths rather than the sharp difference in floral composition that is now evident.

Upon return to the laboratory the algae were identified and mounted on herbarium sheets for permanent retention in the Laboratory's herbarium. Thirty of the microscopic forms were unfortunately discarded after the identification (footnoted in Table II).

DESCRIPTION OF THE HABITAT

Most of the stations were located 240° (magnetic) off Johns Pass, Madeira Beach. Some stations were made at 230°, 235° and 245° off Johns Pass, and one station was located 70° off the southern tip of Egmont Key, approximately 9 miles offshore. The 35 - 40 feet depths were located approximately 9 - 12 miles offshore, and the 45 - 60 feet depths were located approximately 13 - 20 miles offshore.

Three types of substrates were encountered. The first, a flat, shelly and sandy bottom, was generally unproductive, but this bottom type at one location at a depth of 40 feet was found to support a network of *Caulerpa sertularioides*. Collecting was not done on this type of bottom, owing to its general unproductiveness. The second type substrate, an artificial one, consisted of the metallic wrecks of ships. This type was observed to be receptive to algal colonization, and macroscopic red algae were much more abundant on these structures than on rocky reefs. The third type substrate, limestone reefs with heavy incrustations, supported an abundant and varied algal flora. These reefs rise on the average from three to four feet above the rubble and sandy bottom. Most of the collections were made on these reefs. Dr. Robert N.

Ginsburg described a sample of this limestone as a dolomitic calcarenite, possibly of Tertiary age. The area covered by individual reefs varied from a few hundred square feet to an estimated several thousand square feet.

The reefs occur in depths from about 15 feet at one-half mile offshore to a depth and distance as yet undetermined. Operators of fishing party boats report the sporadic occurrence of reef type silhouettes on their fathometers to distances of at least 50 miles out. Jordan (1952) reported a distinctive reef formation 100 miles northwest of Tampa Bay in depths of 18 - 30 fathoms. It is possible that these reefs are an extension of the same formations which we studied.

The reefs in the 15 feet depths were not studied because the turbidity of the water limited visibility to but a few feet or less.

The area surrounding those reefs studied was always covered by a very fine silt which was easily disturbed and would obscure the area, requiring several minutes to clear. This silt was more abundant at the shallower depths. Rubble of shell and pieces of limestone surrounded the reefs. A very soapy type limestone was once noticed under this rubble.

A portion of the material incrusting a reef was examined in the laboratory. The structure was found to consist of an unknown black organic crust overlying a pink crust of *Lithothamnion syntrophicum* which was in cystocarpic state. This algal crust was solid but was also present as flecks to a depth of 4 mm from the surface. Other organic material found in the upper 4 mm were: filamentous red and blue-green algae, bryozoans, and worm tubes. In some parts the rock was riddled by the tubes of polychaetous annelids and pholadids. Major incrusting forms on the reefs also included the mollusks *Arca* and *Spondylus*, and a number of alcyonarians and small hard corals.

Bottom detritus was dissolved in nitric acid. A residue remained which consisted of sand-like particles 105 - 210μ in diameter, with a few particles ranging from 1300 - 1400μ in diameter. A very minute portion of the residue appeared to be organic in nature.

Although no Secchi disc readings were made, it was observed that the water was always much clearer in the 45 - 60 feet depths than in the 35 - 40 feet depths. This is related to the more abundant accumulation of silt around the reefs in the shallower depths and the fact that deeper waters are less subject to turbulence. Lateral visibility in the shallower depths was estimated to be about 10 - 20 feet. Once during a period of 20 mph northwest winds visibility was less than one foot on the bottom at 35 feet. In depths of 45 - 60 feet the lateral visibility was about 35 - 40 feet and never was as poor as in the 35 - 40 feet depths.

The St. Petersburg Field Station, U. S. Fish and Wildlife Service, initiated monthly hydrographic sampling stations in the Gulf of Mexico west of Egmont Key in October, 1958. Egmont Key is approximately 11 miles south of Johns Pass. Both surface and bottom temperatures, taken during the study, were generously contributed for

use in this paper. During the period of October, 1958, through September, 1959, the month of coldest water was January. In this month the surface reading was 13.7°C. and 15.8°C. in approximately 35 feet of water, 10 miles west of Egmont Key; at 20 miles west of the Key, in approximately 55 feet of water in January, 1959, the surface reading was 15.2°C. and 16.5°C. at the bottom. The warmest month was July, 1959. At 10 miles offshore the surface reading was 30.6°C. and was 30.6°C. in 35 feet of water; at 20 miles offshore the surface reading was 30.2°C. and 30.1°C. in 55 feet of water. The most conspicuous element in this data is the lack of differential between surface and bottom temperatures in both depths throughout the year. The temperatures were taken in the field by a Whitney Thermistor, a continuous recording device. Because of the lack of information on bottom water temperatures in the Gulf of Mexico, the temperatures recorded for the two above described locations will be listed in Table I.

A surface current of about 2 mph was usually present in the area studied. When present the direction of the current was always toward the north.

RESULTS

The species list and data are given in Table II. The following abbreviations are used to denote abundance: V — very common, U — uncommon, C—common, R— rare. A blank in this column indicates that no observations were made.

All plants were either attached to the bottom, to other algae, or occurred entangled among other algae.

A total of 158 taxa of algae were obtained. Of these, eight were

TABLE I.—Water temperatures (unpublished data from St. Petersburg Field Station, U.S. Fish and Wildlife Service)

Date	35 feet deep		55 feet deep	
	Surface	Bottom	Surface	Bottom
Oct. 1958	29.0	29.0	29.0	29.0
Nov. 1958	23.0	23.0	24.5	25.1
Dec. 1958	21.5	21.9	22.3	22.6
Jan. 1959	13.7	15.8	15.2	16.5
Feb. 1959	19.4	19.0	21.0	17.0
Mar. 1959	18.7	18.7	20.4	20.1
Apr. 1959	20.7	20.0	20.1	19.4
May 1959	23.9	23.6	23.9	22.0
Jun. 1959	27.9	27.8	27.5	26.6
Jul. 1959	30.6	30.6	30.2	30.1
Aug. 1959	28.9	28.9	29.4	29.8
Sep. 1959	27.9	28.1	28.1	27.8

identified only to genus and one only to the family because the specimens lacked critical taxonomic characters.

Ninety-five taxa were found at the 35 - 40 feet stations, of which seven were identified only to genus. One hundred and eleven taxa were found at the 45 - 60 feet stations of which six were identified only to genus and one only to the family.

Species found only on the metal wrecks are footnoted in Table II. *Caulerpa sertularioides* was found on sand on June 18, 1958. All other collections came from the limestone reefs.

TABLE II.—Species list

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
CYANOPHYCEAE					
Anacystis marina Dr. & Daily[1]	55-60	5-X-58	R	*	
**Calothrix pilosa* Harv.[3]	40	7-XII-58	U	*	
**Hydrocoleum penicillatum* Taylor[2]	50	2-V-59	C	*	
Lyngbya confervoides C. Ag.[2]	60	9-VIII-58		*	
L. gracilis (Menegh.) Rab.	35	8-II-59	C	*	
	55	31-I-59	V	*	
	55-60	5-X-58	V	*	
L. majuscula Harv.[2]	35	17-VIII-58		*	
	55	7-X-58		*	
	55-60	21-X-58	V	*	
**L. meneghiniana* Kutz. Gom.	38	14-II-58	C	*	
L. mittsii Phillips	40	7-XII-58	V	*	
**L. rosea* Taylor[3]	60	9-IX-58		*	
L. sordida (Zanard.) Gom.	35	3-I-59	C	*	
	35	8-II-59	U	*	
	38	14-II-59	U	*	
	40	7-XII-58	U	*	
L. sordida fa. *bostrychicola* (Crouan) Gom.[1]	55-60	5-X-58	U	*	
Mastigocoleus testarum Lagerheim[2]	38	14-II-59	V		
	55	31-I-59	U		
Microcoleus chthonoplastes (Fl. Dan.) Thur.	40	7-XII-58	U	*	
Phormidium papyraceum (C. Ag.) Gom.	50	2-V-59	C	*	
P. submembranaceum (Ard. et Straff.) Gom.[3]	45-50	23-XI-58	U	*	
Plectonema nostocorum Born.	38	14-II-59	V	*	
	40	7-XII-58	V	*	
	55-60	5-X-58	C	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
Skujaella thiebautii DeToni[3]	45	29-VI-58	C		
Spirulina subsalsa Oerstedt fa. *oceanica* (Crouan) Gom.[1, 2]	55-60	5-X-58	U	*	
CHLOROPHYCEAE					
Acetabularia crenulata Lamx.[2]	40	18-VI-58			
**Avrainvillea asarifolia* Børgs.[1]	55-60	5-X-58			
**A. nigricans* Decaisne	55	7-IX-58			
**Bryopsis plumosa* (Huds.) C. Ag.	35	7-II-59	R	*	
Caulerpa crassifolia (C. Ag.) J. Ag. fa. *mexicana* (Sonder) J. Ag.	38	14-II-59	U		
	45	29-VI-58			
C. crassifolia (C. Ag.) J. Ag. fa. *typica* (Weber) Børgs.	40	7-XII-58			
	55	7-IX-59			
	55-60	5-X-58			
C. cupressoides (West) C. Ag. var. *elegans* (Crouan) Weber	45-50	23-XI-58	U		
C. paspaloides (Bory) Grev. var. *typica* Weber.	35	13-VII-58			
C. peltata (Turn.) Lamx.	60	19-VIII-58			
	55	7-IX-58			
	55-60	21-IX-58			
	55-60	5-X-58			
C. prolifera (Førsskal) Lamx.	35	13-VII-58			
C. sertularioides (Gmel.) Howe	40	18-VI-58			
	35	13-VII-58			
	39	19-XI-58	V		
	40	7-XII-58	U		
	55	31-I-59			
	60	9-VIII-58			
	55	7-IX-58			
	55-60	5-X-58			
C. sertularioides (Gmel.) Howe fa. *brevipes* (J. Ag.) Sved.	38	19-II-59	U		

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
C. sertularioides (Gmel.) Howe fa. *longipes* (C. Ag.) Collins	38	19-II-59	U		
	50	2-V-59	R		
**Cladophora glaucescens* (Griff.) Harv.	35	13-VII-58		*	
Codium isthmocladum Vick.	35	8-II-59			
	38	19-II-59	V		
	35	17-VIII-58			
	39	9-XI-58	R		Gametangia
	40	7-XII-58	U		Gametangia
	55	31-I-59	R		
	50	2-V-59	U		
	60	9-VIII-58		*	
	55	7-IX-58			
	55-60	21-IX-58			
	55-60	5-X-58		*	
**C. repens* ? (Crouan) Vick	35	8-II-59			
	60	25-IV-59	R		
	50	2-V-59	R		
C. taylori Silva	35	8-II-59			
	35	13-VII-58			
	35	17-VIII-58			
**Derbesia vaucheriaeformis* (Harv.) J. Ag.[1]	35	17-VIII-58	U	*	
Entocladia wittrockii Wille	40	7-XII-58	V	*	
**Ernodesmus verticillata* (Kutz.) Børgs.[2, 3]	40	7-XII-58	R	*	
Halimeda discoidea Decaisne	55	7-IX-58			
**H. opuntia* (L.) Lamx. var. *typica* Barton	40	18-VI-58			
	55	27-IV-58	U		
**H. scabra* Howe	35	13-VII-58			
	39	9-XI-58	C		
	40	7-XII-58	V		
	55	31-I-59	V		
	58	9-IV-59	V		
	60	25-IV-58	V		
	55	27-IV-58	C		
	50	2-V-59	V		
	48	24-V-59	V		
	60	9-VIII-58	C		Sporangia
	55	7-IX-58			
	55-60	5-X-58			
	45-50	23-XI-58	V		

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
Penicillus capitatus Lamarck[2]	60	9-VIII-58			
	55	7-IX-58			
Unidentified species of Chaetophoraceae[4]	55	27-IV-58	U		
**Rhipocephalus oblongus* (Decaisne) Kutz.[2]	40	18-VI-58			
	60	9-VIII-58			
	55-60	5-X-58			
**R. phoenix* (E. & S.) Kutz. fa. *typicus* Gepp.	55	31-I-59			
	58	9-IV-59	C		
	60	25-IV-58	V		
	50	2-V-59	V		
	48	24-V-59	V		
	45	29-VI-58			
	55	7-IX-58			
	45-50	23-XI-58			
Rhizoclonium kerneri Stockmayer	35	8-II-59	R	*	
	55	31-I-59	C	*	
	60	25-IV-59	R	*	
Udotea conglutinata (Solander) Lamx.	40	18-VI-58			
	35	13-VII-58			
	50	2-V-59	U		
	48	24-V-59	U		
	60	9-VIII-58			
	55	7-IX-58			
U. flabellum (E. & S.) Howe	58	11-IV-59	U		
	55	7-IX-58			
	55-60	5-X-58			
**U. spinulosa* Howe	50	2-V-59	U		
**Valonia macrophysa* Kutz.	60	25-IV-59	U		
	55-60	5-X-58			
PHAEOPHYCEAE					
Dictyopteris delicatula Lamx.[1, 2, 3]	55-60	5-X-58	R		
Dictyota cervicornis Kutz.	55	7-IX-58	R		
	55-60	5-X-58	R		
D. dichotoma (Huds.) Lamx.	50	2-V-59	R		Tetrasporic
	60	9-VIII-58			
**D. divaricata* Lamx.	55-60	21-IX-58	R		
	45-50	23-XI-58	C	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
Dictyota sp.	35	13-VII-58	R	*	
	55	7-IX-58	R		
**Dilophus alternans* J. Ag.[3]	40	7-XII-58	R		
Ectocarpus duchassaingianus Grun.[2]	40	18-VI-58		*	Pleurilocular sporangia
Ectocarpus sp.	40	18-VI-58	V		
	45	24-VI-58	V		
**Eudesme howei* Taylor[3]	40	18-VI-58		*	Sporangia
E. zosterae (J. Ag.) Kylin[3]	50	2-V-59	R	*	
Padina vickersiae Hoyt[3]	40	18-VI-58			Antheridia & oogonia
Sargassum filipendula C. Ag.	35	3-I-59	V		
	35	8-II-59	C		
	38	14-II-59	V		
	39	9-XI-58	V		
	40	7-XII-58	U		
	55	21-I-59	U		
	55	27-IV-58	C		
	58	11-IV-59	C		
	50	2-V-59	V		
S. filipendula C. Ag. var. *montagnei* (Bailey) Coll. & Hervey	35	8-II-59	U		
S. hystrix J. Ag. var. *buxifolium* (Chauvin) J. Ag.	60	9-VIII-58			
	55-60	21-IX-58			
S. lendigerum? (L.) C. Ag.	58	11-IV-59	U		
	55-60	5-X-58			
**S. vulgare* C. Ag.	45-50	23-XI-58	U		
**Spatoglossum schroederi* (Mart.) J. Ag.	35	14-II-59	U		
	38	14-II-59	U		
Sphacelaria furcigera Kutz.[3]	45-50	23-XI-58	U		
RHODOPHYCEAE					
Acrochaetium avrainvilleae Børgs.	40	7-XII-58	V	*	Monospores
A. flexuosum Vick.	35	3-I-59	C	*	Monospores
A. netrocarpum Børgs.	40	18-VI-58		*	
A. phacelorhizum Børgs.[3]	55	31-I-59	U	*	
A. seriatum Børgs.[3]	35	8-II-59	V	*	Monospores
	38	14-II-59	C	*	Monospores
A. unipes Børgs.	55	27-IV-58	U	*	Monospores

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
Acrochaetium sp.	35	13-VII-58		*	
	60	25-IV-59	C	*	
	50	2-V-59	C	*	
	45	29-VI-58		*	
Acrochaetium sp.	50	2-V-59	C	*	
Agardhiella tenera (J. Ag.) Schmitz	38	14-II-59	C		
	35	13-VII-58			
	35	17-VIII-58			
	39	9-XI-58			
**Amphiroa fragilissima* (L.) Lamx.	55	7-IX-58			Cystocarpic
**A. rigida* Lamx. var. *antillana* Børgs.	60	9-VIII-58			
Botryocladia occidentalis (Børgs.) Kylin	38	14-II-59	U		
	35	17-VIII-58			
	39	9-XI-58	U		Cystocarpic
	40	7-XII-58			
	48	14-V-59	U		
	55-60	5-X-58	C		
Callithamnion byssoides Arnott[3]	35	3-I-59	C	*	
	48	31-I-59	U	*	
C. cordatum ? Børgs.[1, 3]	55-60	5-X-58		*	
C. roseum (Roth.) Harv.[3]	55-60	21-IX-58		*	
Callithamnion sp.	35	17-VIII-58		*	
	55	7-IX-58		*	
Ceramium byssoideum Harv.[2]	40	7-XII-58	V	*	
C. codii (Richards) Mazoyer	35	3-I-59	U	*	
	39	9-XI-58	C	*	
	40	7-XII-58	C	*	Tetrasporic
	55	31-I-59	U-C	*	
	60	25-IV-59	C	*	
	50	2-V-59	V	*	Tetrasporic
**C. corniculatum* Mont.	39	9-XI-58	C	*	
	55-60	5-X-58	V	*	
C. deslongchampsii Chauvin[3]	45	29-VI-58		*	
C. fastigiatum (Roth) Harv. fa. *flaccidum* H. G. Petersen	40	18-VI-58		*	Tetrasporic
**C. floridanum* J. Ag.	55-60	21-IX-58		*	
C. subtile J. Ag.[2, 3]	55	31-I-59	C	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
C. tenuissimum (Lyngbye) J. Ag.	35	3-I-59	R	*	
	38	14-II-59	V	*	Tetrasporic
	40	18-VI-58		*	Tetrasporic
	35	13-VII-58		*	
	55	31-I-59	C	*	
	50	2-V-59	U	*	
	48	24-V-59	U	*	
	60	9-VIII-58		*	
	55	7-IX-58	V	*	
Champia parvula (C. Ag.) Harv.	35	3-I-59		*	
	35	8-II-59	R	*	
	40	18-VI-58		*	
	35	17-VIII-58	U	*	
	39	9-XI-58		*	
	40	7-XII-58	U	*	
	50	2-V-59	R	*	
	60	9-VIII-58		*	Cystocarpic
	55	7-IX-58		*	
Chondria dasyphylla (Woodward) C. Ag.[2, 3]	40	18-VI-58			Cystocarpic
Chrysymenia enteromorpha Harv.	50	2-V-59	R		
Crouania attenuata (Bonne.) J. Ag.	35	3-I-59	U	*	Tetrasporic
	60	9-VIII-58		*	Cystocarpic, antheridial
	55	7-IX-58		*	Tetrasporic
Dasyopsis antillarum Howe[3]	38	14-II-59	R		Tetrasporic
Digenia simplex (Wulf.) C. Ag.[2]	60	25-IX-59	U		
**Dudresnaya caribaea* (J. Ag.) Setch.[3]	40	18-VI-58		*	Cystocarpic
Erythrocladia subintegra Rosenvinge	38	14-II-59	C	*	
	40	7-XII-58	C	*	
	55-60	5-X-58	C	*	
Erythrotrichia carnea (Dillw.) J. Ag.	35	3-I-59	R	*	
	35	8-II-59	R	*	
	38	14-II-59	C	*	
	40	18-VI-58		*	
	35	13-VII-58		*	
	40	7-XII-58	R	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
	60	25-IV-59	U	*	
	55	27-IV-58	C	*	
	50	2-V-59	U	*	
Eucheuma ancanthocladum (Harv.) J. Ag.	35	13-VII-58			
**E. isiforme* (C. Ag.) J. Ag.	35	8-II-59	C		Cystocarpic
	38	14-II-59	U		
	35	17-VIII-58			
	39	9-XI-58	R		
	40	7-XII-58	U		
	55-60	21-IX-58			
	55-60	5-X-58			
	45-50	23-XI-58			
Fosliella farinosa (Lamx.) Howe var. *solmsiana* (Falkenberg) Taylor[1, 2]	55-60	5-X-58	V	*	
F. lejolisii (Rosanoff) Howe	35	3-I-59	V	*	Cystocarpic
	35	8-II-59	V	*	
	38	14-II-59	V	*	Cystocarpic
	40	18-VI-58		*	
	39	9-XI-58		*	Cystocarpic
	40	7-XII-58	C	*	
	55	31-I-59	V	*	
	60	25-IV-59	V	*	
	50	2-V-59	V	*	
	60	9-VIII-58		*	
	55	7-IX-58		*	
	45-50	23-XI-58	V	*	Cystocarpic
Gelidium pusillum (Stackhouse) LeJolis[1, 2, 3]	55-60	5-X-58			
Goniolithon decutescens (Heydrich) Foslie[2]	60	9-VIII-58			
**G. solubile* Foslie & Howe[2]	35	8-II-59	C		
	50	2-V-59	V		Cystocarpic
Goniotrichum alsidii (Zanard.) Howe	38	14-II-59	R	*	
	50	2-V-59	C	*	
**Gracilaria bursa-pastoris* (Gmel.) Silva	40	7-XII-58	U		Cystocarpic
**G. cervicornis* (Turn.) J. Ag.[1]	55-60	5-X-58	C		Cystocarpic, tetrasporic
G. cornea J. Ag.[2]	60	9-VIII-58			
	55	7-IX-58			

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
**G. curtissiae* J. Ag.	60	9-VIII-58			
**G. cylindrica* Børgs.[1]	55-60	5-X-58			
G. ferox J. Ag.	38	14-II-59	U		
	40	7-XII-58	U		
	55-60	5-X-58	V		Cystocarpic
**G. mamillaris* (Mont.) Howe	35	17-VIII-58			
	40	7-XII-58	U		
G. verrucosa (Huds.) Papenf.	35	13-VII-58			
Gracilaria sp.	38	14-II-59			
**Griffithsia globulifera* Harv.	35	3-I-59	R	*	
	35	8-II-59	U	*	
	40	7-XII-58	R	*	
	60	9-VIII-58		*	Tetrasporic
	55	7-IX-58		*	Tetrasporic
	45-50	23-XI-58	R	*	
Grinnellia americana (C. Ag.) Harv. var. *caribaea* Taylor	38	14-II-59	C		Tetrasporic
Halymenia agardhii DeToni	35	13-VII-58			
H. floresia (Clemente) C. Ag.	35	13-VII-58			
	60	9-VIII-58			
	55	7-IX-58			
H. gelinaria Collins & Howe	55-60	21-IX-58			
	39	9-XI-58	R		
	40	7-XII-58	R		
	55-60	21-IX-58			Cystocarpic
H. pseudofloresia Collins & Howe	38	14-II-59	U		
	35	13-VII-58			
	55-60	5-X-58	C		
**Hildenbrandtia prototypus* Nardo[2]	60	25-IV-59	C		
	55-60	5-X-58	V		
**Hypoglossum tenuifolium* (Harv.) J. Ag.	60	9-VIII-58			Tetrasporic
**Jania adhaerens* Lamx.	40	18-VI-58		*	Cystocarpic
	60	25-IV-59	U		
	60	9-VIII-58		*	Cystocarpic
J. capillacea Harv.[3]	40	7-XII-58	C	*	
J. pumila Lamx.[2, 3]	40	7-XII-58	C	*	
Laurencia gemmifera Harv.	50	2-V-59		*	Tetrasporic
	60	9-VIII-58			

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
L. intricata Lamx.	55	7-IX-58			
L. obtusa (Huds.) Lamx.	55	31-I-59			
**L. papillosa* (Førsskal) Grev.[2]	38	14-II-59	R		
	60	25-IV-59	C		
	55	27-IV-58	R		
L. poitei (Lamx.) Howe	40	18-VI-58			
	40	7-XII-58	U		
	50	2-V-59	U		Tetrasporic
	45	29-VI-58			
	60	9-VIII-58			
Laurencia sp.	35	8-II-59	R	*	
	35	13-VII-58	R	*	
Lithothamnion occidentale Foslie	60	25-IV-59	C		
**L. syntrophicum* Foslie	38	14-II-59	V		Cystocarpic
	60	25-IV-59	C		Tetrasporic
Lophosiphonia scopulorum (Harv.) Womersley	40	7-XII-58	U	*	Cystocarpic
**Melobesia membranacea* (Esper) Lamx.	55	31-I-59	C		
	55	27-IV-58	U		
**Meristotheca duchassaignii* J. Ag.[1]	35	17-VIII-58			
Mesothamnion caribaeum Børgs.[3]	40	7-XII-58	R	*	
Peyssonnelia rubra (Grev.) J. Ag.	38	14-II-59	U		
	55	7-IX-59			
Polysiphonia binneyi Harv.	35	13-VII-58			Tetrasporic
	55	7-IX-58		*	Cystocarpic
**P. denudata* (Dillwyn) Kutz.[3]	45	29-VI-58		*	
**P. gorgoniae* Harv.[3]	55	31-I-59	U	*	Cystocarpic
**P. hapalacantha* Harv.[3]	40	18-VI-58			
P. havanensis Mont.	55-60	21-IX-58		*	
	45-50	23-XI-58		*	
P. howei Hollenberg	60	9-VIII-58		*	Cystocarpic
P. macrocarpa Harv.[2]	35	6-I-59	U	*	
	35	8-II-59	R	*	
	38	14-II-59	U	*	
	40	7-XII-58	U	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
Polysiphonia sp.	35	13-VII-58			Tetrasporic
Rhabdonia ramosis-	60	9-VIII-58		*	
sima (Harv.) J. Ag.	40	7-XII-58	U		Cystocarpic
	55-60	21-IX-58			
Scinaia complanata (Collins) Cotton					
var. *intermedia* Børgs.	38	14-II-59	R		Cystocarpic
	40	18-VI-58			Cystocarpic
**Seirospora*					
occidentalis Børgs[1, 3]	55-60	5-X-58		*	Cystocarpic
Spermothamnion gorgoneum					
(Mont.) Born.[2]	39	9-XI-58	V	*	Polyspores
**S. investiens*					
(Crouan) Vick.	60	9-VIII-58		*	
	55	7-IX-58		*	
**S. investiens* (Crouan) Vick.					
var. *cidaricola* Børgs.	50	2-V-59	V	*	
Spyridia fila-					
mentosa (Wulf.) Harv.	35	3-I-59	R	*	
	35	13-VII-58			
	39	9-XI-58			
	60	9-VIII-58		*	Cystocarpic
	55	7-IX-58	V		
	55-60	21-IX-58			
Wurdemannia miniata (Drap.) Feldmann					
& Hamel	55-60	5-X-58			

* Not previously reported north of the Dry Tortugas on the Florida Gulf coast.

[1] Species found only on metal wrecks.

[2] Species found only in very shallow water at the Dry Tortugas [as reported by Taylor (1928)].

[3] Species not in herbarium.

[4] Material examined by Dr. H. J. Humm. The plant does not have setae. Dr. Humm stated that each cell is extended on the top side into a peak or point. No confidence is placed on identification beyond the family.

DISCUSSION

A very interesting algal association was noted in the 45 - 60 feet depths where a vast carpet of *Halimeda scabra,* composed of plants two to three inches tall, was found on the reefs. *Rhipocephalus phoenix typicus* was usually associated with the *Halimeda,* but was

not as abundant. *Sargassum filipendula* was also abundant, not on the reef, but on the detritus-covered hard bottom surrounding it. These attached *Sargassum* plants, mostly from two to three feet high, occurred one plant every square meter over very large areas, but on several occasions no plants were found. This association was not seen in the 35 - 40 feet depths. *Sargassum filipendula* was found at 5 of the 8 stations in 35 - 40 feet and is considered to be a characteristic plant of these shallower depths. *Halimeda scabra* was found in only 3 of the 8 collections in this depth range and was abundant at only one of these. *Rhipocephalus phoenix* was not found at the 35 - 40 feet depths, but *R. oblongus* occurred in one collection in which it was associated with *Halimeda opuntia typica.*

Several species of *Goniolithon* and *Lithothamnion* were occasionally observed as large knobby growths on the rocky reefs. It is believed that these crustaceous coralline algae are probably an important constituent of the reef flora, however, due to the lack of attention to these algae, we cannot elaborate on this.

Despite the fact that most collections were made on the limestone reefs, several species of Codiaceous green algae with rhizoidal systems were found, often in great abundance. Plants of *Halimeda scabra* and *Udotea flabellum* were attached directly to the hard rock surface. The other species of this group, *viz., Caulerpa* spp., *Halimeda* spp., *Rhipocephalus* spp., *Udotea* spp., *Penicillus capitatus,* and *Avrainvillea* spp., had extremely fine shell detritus and sand grains bound up in the rhizoids. The reef surface was never smooth, but was extremely pitted and craggy. Detritus and sand evidently collected in the rock depressions and potholes, and these algae which are anchored by rhizoids probably invaded the reefs by growing in the detritus filled depressions.

A large number of algal species were found at the 35 - 40 feet depths, but excepting *Sargassum filipendula,* none seemed particularly conspicuous. Once during a storm, vast amounts of *S. filipendula* were found floating on the surface over 35 feet of water. These plants had holdfasts and were in a fresh condition. Reefs were present on the bottom in the vicinity of this floating mass, and it is possible that the rough water may have torn the plants loose from the bottom.

Many more species of red algae were found in the 35 - 40 feet depths than any other group; however, of the macroscopic algae no group appeared to be dominant at a particular station. The epiphytic flora in the 35 - 40 feet depths was a major constituent of the species. Three species of macroscopic algae supported most of these epiphytes: *Halimeda scabra, Sargassum filipendula,* and *Codium isthmocladum,* none of which are red algae.

In contrast to the 35 - 40 feet depths is the 45 - 60 feet range in which *Halimeda, Rhipocephalus,* and *Sargassum* usually dominated the algal biomass present on the rocky reefs. This excludes considera tion of the encrusting coralline red algae. In terms of biomass the

macroscopic reds were very scarce. Species-wise the red algae comprised over half the total.

On two occasions the junior author collected on metal shipwrecks. One wreck was at a depth of 32 - 35 feet and the other was at 60 feet. Although portions of these wrecks rose as much as 20 feet off the bottom, only the algae within two or three feet of the bottom were collected. At both stations the red algae appeared to comprise the major portion of the algal biomass. *Sargassum* was not present about the shallower wreck and only sparse plants of *S. lendigerum* were present around the deeper one. The holdfast type base of the macroscopic red algae appears to be better suited for colonization on hard surfaces such as metal than does the rhizoid type base of the Codiaceous green algae. Wherever ship wrecks are found in the shallow waters of the Gulf of Mexico, red algae should be expected to prevail.

Eleven species are newly reported for Florida. These are: *Sargassum lendigerum* (?), *Acrochaetium avrainvilleae, A. netrocarpum, A. phacelorhizum, A. seriatum, A. unipes, Callithamnion cordatum, C. roseum, Ceramium codii, Mesothamnion caribaeum,* and *Lophosiphonia scopulorum.* Forty-seven species (marked by an asterisk in Table II) have not been previously reported north of the Dry Tortugas on the Florida Gulf coast and thus represent northward range extensions.

TABLE III.—Synopsis of species

Depth Range (Feet)	35-40		45-60
Total taxa of Cyanophyceae	9		13
Total taxa of Chlorophyceae	21		23
Total taxa of Phaeophyceae	9		12
Total taxa of Rhodophyceae	56		63
TOTAL	95		111
Taxa not found at other depth range	47		63
Taxa found at both depth ranges		48	
Taxa of Rhodophyceae not found at other depth range	27		34
Taxa of Rhodophyceae found at both depth ranges		29	
Taxa of epiphytes not found at other depth range	27*		31*
Taxa of epiphytes found at both depth ranges		19	
Per cent of taxa which were rhodophycean epiphytes	31		31
Per cent of epiphytes which were Rhodophyceae	63		68

* Four taxa were found in both depth ranges, one was an epiphyte in the 35-40 feet range only, and three were epiphytes in the 45-60 feet range only.

A summary of much of the information obtained in the present study is contained in Table III. The most obvious and interesting conclusion is that despite the differences, species-wise, between the two depth ranges considered, the composition of the algal flora is essentially the same in both. That is, both the ratios of the major algal groupings (Classes) and the ratios of the epiphytes remain constant.

In Table IV we have grouped data reported by Taylor (1928) for comparison with similar data in our Table III. It can be seen that the Tortugas algae also hold, at least in the shallower depths comparable to ours, a more or less constant relationship between the various groupings, though not of the same ratios as ours. These constant relationships at the different depths, although including different species, seem to denote that they are more than just a function of the number of possible species. The factors which might regulate these relationships are unknown to us.

More extensive collecting must be done in order to reveal possible seasonal variation in plant abundance and/or occurrence. The records collected thus far do not indicate such variation.

Taylor (*op. cit.*) recorded only 60 per cent of the taxa listed in Table II from the Dry Tortugas. It is interesting to note that 28 of the taxa we list (footnoted in Table II) were found by Taylor only in much shallower water. It has been the junior author's experience with fishes that several species found locally only in deep water are recorded from very shallow depths at Tortugas. Taylor emphasized the biomass dominance of the green algae in depths comparable to ours, but called attention to the fact that the number (taxa) of red algae greatly exceeded the number of green algae. Our findings are in accord with his.

SUMMARY

Marine algae were collected on limestone reefs in water 35 - 60 feet deep in the Gulf of Mexico off Pinellas County, Florida, over a period of one year. SCUBA type diving equipment was used.

Two depth ranges were chosen, owing to the assemblage of plants found in each. The first was 35 - 40 feet, and the second was 45 - 60 feet. Ninety-five taxa were found in 35 - 40 feet in eight collections. One hundred and eleven taxa were found in 45 - 60 feet in twelve collections. A total of 158 taxa of plants were found during the study.

TABLE IV.—Comparative data on depth from Dry Tortugas (extracted from Taylor, 1928, Table 6)

Depth (meters)	3.1	9.2	18.3	36.6	55	73.2	91.5
Total taxa of Cyanophyceae	2	3	3	3	–	–	–
Total taxa of Chlorophyceae	27	34	24	17	13	10	9
Total taxa of Phaeophyceae	14	17	16	6	1	1	1
Total taxa of Rhodophyceae	52	56	46	24	7	3	-

The red algae, though high in species numbers, were small in biomass in both depths. However, when metal wrecks were encountered, it was observed that the biomass of red algae was large. *Sargassum filipendula,* owing to the regularity with which it was found in 35 - 40 feet, is considered a characteristic plant in this depth range. No other algal complex or species was observed to dominate on the reefs in this depth.

Vast carpets of *Halimeda scabra* were observed at most of the 45 - 60 feet stations. This species was observed to be characteristic of this depth. *Rhipocephalus phoenix* and *Sargassum filipendula* were often associated with *Halimeda.*

The epiphytic flora, a large percentage of which were red algae, accounted for nearly one-half of the total number of species found.

Eleven species are newly reported for the state, and 47 represent northward range extensions from the Dry Tortugas.

On the basis of this study and comparison with the results of Taylor's (1928) work at the Dry Tortugas, a more or less constant relationship between the various algal groupings can be seen. Although different species are included in the two areas, those relationships seem to denote that they are more than just a function of the number of possible species. The factors which might regulate these relationships are unknown to us.

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Ectoparasites of Pocket Gophers From Colorado

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Four species of pocket gopher occur in Colorado — *Cratogeomys castanops* occupies most of the area south of the Arkansas River in Baca, Prowers and Bent Counties and the eastern part of Otero County; *Geomys bursarius* is found throughout most of the plains north of the Arkansas River and east of the front range of the Rocky Mountains; *Thomomys bottae* occurs in the valleys of the southwest, along the front range as far north as Colorado Springs, and from the front range west to Salida; and *Thomomys talpoides* occupies most of the remaining areas (Miller, unpublished).

The ranges of these four species meet in different combinations of contiguous allopatry at various localities along the Arkansas River and in the vicinity of Colorado Springs, thus offering a unique opportunity for studies of their interrelationships. The purpose of this study was a preliminary survey of the ectoparasites of the pocket gophers of Colorado, with special reference to localities where the ranges of the different pocket gophers meet and where host-specificity would best be shown.

Methods

Collections were made in August 1957 at localities selected on the basis of the distributions outlined above. The pocket gopher specimens were placed in individual plastic bags and stored with dry ice until they could be examined. The parasites were removed within one or two days after the gophers were trapped, and were treated in the manner outlined by Ward (1957a). Lice and a few mites and fleas were also recovered from museum skins in the Warren Collection at Colorado College, the U.S. Fish & Wildlife Service collection at the Denver Federal Center, the Denver Museum of Natural History, and Colorado State University.

We would like to express our appreciation to the following who identified the parasites and provided information about their habits and distributions: Phyllis Johnson (Fleas), G. M. Kohls (Ticks) and Russell Strandtmann (Mites). The lice were identified by Ronald A. Ward.

Results

The numbers of ectoparasites and the host species they were collected from are shown in Table I.

TABLE I.—Ectoparasites collected from pocket gophers in Colorado. Values shown are the numbers of individuals of each parasite species collected from each host species, and the number of individuals of the host species (in parentheses) on which the parasite was found.

Ectoparasite Species	*Thomomys bottae*	*Thomomys talpoides*	*Geomys bursarius*	*Cratogeomys castanops*
ACARINA				
Macrocheles sp.		1(1)	1(1)	
Coprholaspis sp.	1(1)			
Haemogamasus ambulans	1(1)	44(13)		1(1)
Ischryopoda armatus	1(1)			
Hirstionyssus geomydis	2(2)	29(10)	1(1)	
Ornithonyssus sp.		1(1)		
Phytoseidae		1(1)		
Garmania ponorum		1(1)		
Haemolaelaps geomys	20(12)	76(23)	92(13)	2(1)
Aulaelaps stabularis		4(2)		
Ixodes sculptus	10(2)	91(18)	2(1)	
Ixodes kingi	9(2)			
Ixodes sp.[1]	41(2)	1(1)		
Dermacentor sp.	1(1)			
Sarcoptidae		1(1)		
Listrophoridae			1(1)	
MALLOPHAGA				
Geomydoecus thomyus		321(73)		
G. chapini		331(67)		
G. californicus	863(50)		122(7)	
G. minor	655(44)			
G. geomydis				204(5)
G. geomydis-californicus[2]			351(17)	
SIPHONAPTERA				
Foxella ignota	49(16)	192(60)	35(11)	1(1)
Dactylopsylla percernis				8(5)
Thrassis petiolatus	1(1)			

[1] Unidentifiable larvae; probably a mixture of *I. sculptus* and *I. kingi*.

[2] See text for discussion of integradation of *G. geomydis* and *G. californicus*.

A brief account of the habits and host-associations of the ectoparasites is given in the following section:

MITES AND TICKS (ACARINA)

MACROCHELIDAE

Macrochelid mites occur in soil and on vertebrates and invertebrates. They are probably not parasitic (Baker and Wharton, 1952).

Macrocheles sp.—Two females were found on two specimens of *T. talpoides*.

Coprholaspis sp.—One female was found on *T. bottae*.

HAEMOGAMASSIDAE

These mites are common parasites of small mammals throughout the world, which suggests that they may be important in the transmission of plague, typhus, tularemia, and perhaps other diseases (Baker and Wharton, 1952). They attach to the host only to feed; non-feeding time is spent in the nest of the host.

Haemogamasus ambulans (Thors.)—This genus is restricted to small, burrowing rodents and insectivores (Ewing, 1929). *H. ambulans* was common on *T. talpoides* and single specimens were collected from *T. bottae* and *C. castanops*.

Ischryopoda armatus Keegan.—Only two species of this genus are known. *I. armatus* was described from *Thomomys bottae* in California and has also been found in *Dipodomys, Perognathus* and *Peromyscus* from California, New Mexico and Colorado. One specimen was collected from *T. bottae* in this study.

DERMANYSSIDAE

Dermanyssid mites are thought to be relatively specific and the family contains several species of medical and veterinary importance (Baker and Wharton, 1952).

Hirstionyssus geomydis (Keegan).—This genus is almost entirely restricted to rodents (Baker and Wharton, 1952), living in the host nest and attaching to the host only to feed. *H. geomydis* was common on *T. talpoides* and was also present on *T. bottae* and *G. bursarius*.

Ornithonyssus sp.—Members of this genus are true parasites of birds, mammals and reptiles. One specimen was found on *T. talpoides*.

PHYTOSEIDAE

Members of this family are frequently found on plants as predators of plant-feeding invertebrates. One unidentified specimen was found on *T. talpoides*.

Garmania ponorum (Ouds.).—Since members of this genus are non-parasitic, this mite would probably occur on small mammals by accident, or as a predator of other small arthropods. One specimen was found on *T. talpoides*.

LAELAPTIDAE

Laelaptid mites are common, relatively specific, ectoparasites of mammals.

Haemolaelaps geomys Strandtmann.—The genus *Haemolaelaps* occurs on birds and mammals and some species of the genus are apparently restricted to a single genus or family of mammals. *H. geomys* is found only on geomyids and occurs throughout the host range. This species was found on all four species of pocket gophers examined.

Eulaelaps stabularis (Koch).—This species was found on only two specimens of *T. talpoides*. It is associated with various small mammals in Europe and North America. Jameson (1950) found it commonly on *Blarina brevicauda* in California.

IXODIDAE

Ixodes sculptus Neumann.—This tick is common on ground squirrels and their predators throughout the central and western United States and Canada (Gregson, 1956) and was the most common tick found in this study. Tryon (1947) found *Ixodes* sp. common on *T. talpoides* in Montana, but Howard and Childs (unpublished) found no ticks on *T. bottae* in California, even though a careful search was made for them. *I. sculptus* was especially common on *T. talpoides* in this study, but was also found on *T. bottae* and *G. bursarius*. Male *Ixodes* remain on the host only during mating, but females oviposit on the host for several weeks, or even months. No males were collected.

Ixodes kingi Bishop.—This tick is also a common parasite of ground squirrels and their predators in the prairies of the United States and Canada. It was found only on *T. bottae*.

Dermacentor sp.—A single, unidentifiable, larva was collected from *T. bottae*. Species of this genus are not separable at the larval stage, but the larva was either *D. parumapterus* or the Rocky Mountain wood tick, *D. andersoni*. These ticks feed on any of a wide range of hosts and often require a new host for each instar (Gregson, 1956).

SARCOPTIDAE

Sarcoptid mites are skin parasites of warm-blooded animals. The family includes the scabies mite, *Sarcoptes scabiei,* and several other species responsible for sarcoptic mange. One unidentified sarcoptid was found on *T. talpoides*.

LISTROPHORIDAE

Members of this family occur in the hair of small to medium-sized mammals. They apparently feed on sebaceous secretions (Trouessart, 1918). One female, probably *Mycoptes* sp., was found on a specimen of *G. bursarius*.

LICE (MALLOPHAGA)

Since lice spend their entire life cycle on the host, they have been free to evolve a high degree of host specificity. Hopkins (1949) examined 50 species of wild mammals and found only six instances of the same trichodectid on two host species. In each case, closely allied species of the same genus of mammal were involved. This close association between lice and their hosts has also allowed the lice to evolve with their hosts, so that the origins of the host genera and families, and the history of their subsequent distributions, determine whether they are hosts to Anoplura or Mallophaga (Jellison, 1942). The Geomyidae are hosts to Mallophaga but not Anoplura.

TRICHODECTIDAE

Trichodectid lice are common parasites of mammals and usually show a high degree of host-specificity (Hopkins, 1949).

Geomydoecus californicus (Chapman).—Hopkins (1949) lists *Thomomys bottae* as the true host of this species, although it has also been recorded from *Geomys arenarius* and *T. baileyi*. It seems to be a common parasite of *T. bottae* throughout its range in Colorado, and was also collected from *Geomys bursarius* in the vicinity of Colorado Springs and Canon City, where the ranges of *G. bursarius* and *T. bottae* meet.

Geomydoecus chapini Werneck.—The only previous record of this species is from a specimen of *Geomys personatus* from Tabasco, Mexico (Hopkins and Clay, 1952). On the basis of fresh specimens and museum skins examined during this study, this species appears to be generally distributed in Colorado as a parasite of *T. talpoides*. The northern limit of its range is not known. The

junior author examined a large series of museum skins of pocket gophers from Utah and *Geomydoecus chapini* was not found. This may be a species of Mexican origin which has followed the Rocky Mountain chain northward.

Geodmydoecus geomydis (Osborn).—Hopkins (1949) lists *Geomys bursarius* as the true host of this species. There are several records of this louse from *Cratogeomys castanops* however, and it is the only louse known to occur on this genus of pocket gophers. *Geomydoecus geomydis* was not collected from *Geomys bursarius* during this study, but it occurred on all of the *Cratogeomys castanops* examined.

Geomydoecus minor Werneck.—Hopkins (1949) lists *Thomomys baileyi* as the host of *Geomydoecus minor*. It was common on the *T. bottae* specimens examined and seems to occur on this gopher throughout its range.

Geomydoecus thomyus (McGregor).—Hopkins (1949) lists *Thomomys talpoides* as the true host of this species, but it has also been recorded from *Thomomys bottae* and from *Thomomys monticola* in Oregon. This louse is widely distributed throughout the range of *T. talpoides* in the United States and Canada.

Geomydoecus geomydis-californicus.—*Geomys bursarius* is considered to be the true host of *Geomydoecus geomydis* and *Thomomys bottae* the true host of *Geomydoecus californicus* (Hopkins, 1949). None of the *Geomys bursarius* collected during this study were hosts of *Geomydoecus geomydis*, which occurred,

TABLE II.—Relative host specificities of ectoparasites of pocket gophers

	Primarily restricted to Geomyidae	General rodent parasites	Non-parasitic or accidental
MITES	*Hirstionyssus geomydis*	*Haemogamasus ambulans*	*Macrocheles* sp.
	Haemolaelaps geomys	*Ischryopoda armatus*	*Coprholaspis* sp.
		Eulaelaps stabularis	*Garmania panorum*
		Ornithonyssus sp.	
TICKS		*Ixodes sculptus*	
		I. kingi	
		Dermacentor sp.	
LICE	*Geomydoecus californicus*		
	G. chapini		
	G. geomydis		
	G. minor		
	G. thomyus		
FLEAS	*Foxella ignota*	*Thrassis petiolatus*	
	Dactylopsylla percernis		

instead, on *Cratogeomys castanops*. Specimens of *Geomys bursarius* collected in the vicinity of Colorado Springs and Canon City, near the range of *T. bottae*, were hosts to typical *Geomydoecus californicus*. Specimens collected north of these localities, along the front range of the Rocky Mountains, had lice which appeared to be intergrades between *Geomydoecus geomydis* and *Geomydoecus californicus*. These localities represent the western limit of the range of *Geomys bursarius*, and the lice that were collected probably represent a case of introgression.

FLEAS (SIPHONAPTERA)

CERATOPHYLLIDAE

Foxella ignota (Baker).—Fleas of this genus are true parasites of pocket gophers, although they also occur on pocket gopher predators and rodents which are closely associated with pocket gophers and use their abandoned burrows. *Foxella ignota* is widely distributed in the United States, Canada and Mexico, wherever pocket gophers occur, and has also been recorded from ground squirrels, weasels, burrowing owls, pocket mice, prairie dogs and deer mice (Hubbard, 1947). It occurred on all of the species examined in this study.

Dactylopsylla percernis Eads and Menzies.—Fleas of this genus, the "giant fleas of pocket gophers" (Hubbard, 1943), are restricted primarily to the Geomyidae. *D. percernis* was found only on *Cratogeomys castanops* during this study, but this species of flea is relatively rare and individuals generally occur singly or in pairs on the host (Hubbard, 1947). The range of the genus broadly overlaps that of *Foxella*, but *Dactylopsylla* populations are more scattered and less common.

Thrassis petiolatus (Baker).—One specimen was collected from *Thomomys bottae*. This flea is primarily associated with ground squirrels of the genus *Citellus* (Holland, 1949), but has also been collected from woodrats, marmots, cottontails and tree squirrels (Holland, 1949).

On the basis of the data in Table I and the foregoing accounts of the known associations of the ectoparasites collected, the relative host specificities of the ectoparasites are shown in Table II. Two mites, five lice and two fleas are primarily restricted to pocket gophers. Four mites, three ticks and a flea occur on pocket gophers but are known to be general rodent parasites. Three of the mites are considered to be non-parasitic and their occurrence on pocket gophers may have been accidental.

A close correlation was found between adult louse and flea population sizes and the body weights of their hosts, possibly indicating close host-parasite associations (Ward, 1957b). The product-moment correlation coefficients for these relationships are shown in Table III. The correlation coefficient r was computed as explained by Ward (1957b), using the formula:

$$r = \frac{\Sigma\, xy - \bar{x}\, \Sigma\, y}{\sqrt{(\Sigma\, x^2 - \bar{x}\, \Sigma\, x)\,(\Sigma\, y^2 - \bar{y}\, \Sigma\, y)}}$$

The higher correlation between lice and their hosts than between fleas and their hosts may be attributed to a closer parasitic relationship between the former.

TABLE III.—Product-moment correlations between host body weights and adult population sizes of lice and fleas

Host species	Mallophaga n	Mallophaga r	Siphonaptera n	Siphonaptera r
T. bottae	22	0.78	22	0.69
T. talpoides	56	0.60	79	0.59
G. bursarius	12	0.77	12	0.57
C. castanops	6	0.95	6	0.76

DISCUSSION

Various degrees of host-specificity are shown in the ectoparasite fauna of pocket gophers. None of the ectoparasites collected during this study is restricted throughout its range to a single host species, although four species of lice were confined to single hosts during this study. The flea, *Dactylopsylla percernis,* was only collected from *C. castanops,* but is known also from *T. talpoides* and *T. bottae* and the senior author has observed it on other species in Colorado. The fact that it was only recorded on *C. castanops* during this study is probably due to its general scarcity and the short period of time covered by the collections. Thus two mites, five lice and two fleas are primarily restricted to the Geomyidae, but none is restricted to a single species of pocket gopher.

Most of the general rodent parasites were relatively scarce on pocket gophers and occurred on only one or two host species. This was not the case, however, with the mite, *Haemogamasus ambulans,* or the tick, *Ixodes sculptus.* The genus *Haemogamasus* is restricted to burrowing rodents and insectivores, but little is known of the species *H. ambulans.* During this study it was abundant on *T. talpoides* and occurred also on *T. bottae* and *C. castanops. Ixodes sculptus,* a common parasite of ground squirrels, was relatively abundant on *T. bottae* and *T. talpoides* and was also found on *G. bursarius.* In view of their relative abundance on pocket gophers and their host associations during this study, both of these species should probably be considered as common ectoparasites of pocket gophers, even though not primarily restricted to pocket gophers.

Ectoparasite populations would appear to provide excellent material for an evaluation of the role of interspecific competition in animal communities. A fairly wide variety of species is available to the ectoparasite community, the environment is more or less uniform, and the necessary conditions for competition are often present. The evaluation of competition between species has largely been focused upon closely related species of the same genus which might tend to displace one another with respect to a particular ecological niche. Of the fourteen genera of ectoparasite recorded by Jameson (1950) from *Blarina brevicauda,* none was monotypic although six were represented locally by only one species. It was theoretically possible

for the remaining eight genera to have more than one species per genus parasitic on the short-tailed shrews of Jameson's study. However, Jameson (*op. cit.*) concluded that the species within a given family differ in occurrence or in habits, and that they compete on only a limited scale or not at all. In a study of the fleas parasitic on *Apodemus sylvaticus* and *Clethrionomys glareolus*, Evans and Freeman (1950) found as many as four species of flea on an individual host. *Ctenophthalmus agyrtes* and *Malaraeus penicilliger* occurred in sufficient numbers for their associations to be analyzed and were considered to be potential competitors. They showed a strong negative association on *Apodemus* and a moderate positive association on *Clethrionomys*. The authors concluded that the somewhat longer and coarser fur on *Clethrionomys* allowed these two species of flea to live side by side on that host and to avoid the direct competition that might occur on *Apodemus*. When two closely related species are found together on the same host it is often assumed, as in this study by Evans and Freeman (1950), that they occupy different niches and that competition is thus alleviated. Lice have been shown to occupy different ecological niches on birds (Hopkins, 1949; Ward, 1957b), but direct evidence for mammals is lacking. Multiple infestations of lice are common among hyraxes, for example, but it has not been shown that the different genera and species found on these animals prefer different parts of the body.

In the present study only ticks and lice were represented by more than one species of the same genus on a single host. The tick, *Ixodes kingi*, occurred with *I. sculptus* or not at all; although *I. sculptus*, the more abundant of the two, was frequently present when *I. kingi* was absent. There was no apparent tendency for the two species to exclude each other, nor was there any evidence that they occupied different parts of the host.

The lice *Geomydoecus thomyus* and *G. chapini* occurred together on 52.2 per cent of the 92 specimens of *Thomomys talpoides* examined. *G. californicus* and *G. minor* occurred together on 82.7 per cent of the 51 specimens of *T. bottae* examined. The fact that these ectoparasites were not mutually exclusive was also demonstrated by correlations between the numbers of each on a single host individual. The correlation between the numbers of *G. thomomyus* and *G. chapini* on individual *T. talpoides* was 0.46 ($P = .001$). The corresponding correlation for *G. californicus* and *G. minor* on *T. bottae* was 0.63 ($P = .001$). If the members of these species pairs tended to exclude one another, one would expect negative correlations.

The data presented in this study are incomplete with respect to a number of important variables. They are based on collections in selected areas during only one season, and an extended study would show seasonal differences in abundance and distribution of the parasite species, would probably increase the list of ectoparasites known to occur on pocket gophers in Colorado, and might reduce the degree of host specificity shown locally by some species. The extent to which

these data apply to the question of interspecific competition, or lack of it, between closely related species would not be much affected however. There is no doubt that these species exhibit seasonal differences in abundance and have differences in habits — this much can be assumed, *a priori,* from the fact that they are different species. Nevertheless, when an opportunity for competition exists, there is no evidence to show that they exclude each other, or that they occupy niches which are different enough to preclude competition between them.

Summary

A study was made of the ectoparasites of the four species of pocket gopher that occur in Colorado.

Of the ectoparasites collected, two mites, five lice and two fleas are primarily restricted to pocket gophers; four mites, three ticks and one flea are general rodent parasites; and three mites are non-parasitic and may have been accidentals.

Most of the general rodent parasites occurred in small numbers on only one or two host species; but the abundance and host associations of the mite, *Haemogamasus ambulans,* and the tick, *Ixodes sculptus,* suggest that they are common pocket gopher parasites.

Four species of lice were the only ectoparasites that were host-specific, although each of the lice has also been recorded from other hosts in other parts of its range.

There were two examples among the lice and one among the ticks of closely related species of the same genus occurring on the same host. The data showed that these species pairs were not mutually exclusive and there was no evidence that they occupied different ecological niches.

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A Population Study of the Vole, Microtus pennsylvanicus

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Owing to the amount of time and effort required to live-trap small mammals, comparatively little is known concerning the population phenomena of even the more common species. One such species is the meadow vole, *Microtus pennsylvanicus.* Although several studies have been made of this rodent (Gunderson, 1950; Blair, 1948; Hamilton, 1940; Linduska, 1950), for the most part the investigators utilized snap-trapping data or based their results on live-trapping studies in which the intervals between trapping periods were longer than desirable, considering the rate of change of the various population factors. The short life span, as well as the rapid growth and development of *M. pennsylvanicus,* necessitates that samples of the population under study be taken at least at monthly intervals. Studies made at lesser intervals (or continuously) would permit following the population changes even more closely. Since trapping disturbs the population to a certain extent (death of animals in the traps and restriction of movements), intervals of less than one month may result in disturbances sufficient to offset the advantages gained by the closer inspection of the population. Consequently, an interval of approximately one month between trapping periods seems to be a suitable compromise.

The data presented in this paper were obtained during the course of a study of the ecology of *M. pennsylvanicus* in southern Michigan. Other phases of the study, being published separately, include an analysis of the factors influencing the local distribution of the species (Getz, in Press) and its home range, territoriality, and movement (in Preparation).

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Description of the Study Area

Two areas, an abandoned field ("old field") and a marsh, located in the University of Michigan's Mud Lake Research Area, Washtenaw County, Michigan, were studied. The areas were approximately 630 meters apart when measured by the most direct route (through unfavorable *M. pennsylvanicus* habitat), or 1020 meters apart when measured along a more favorable habitat. Although four individuals

moved from one area to the other during the course of the study, the individuals inhabiting each area are considered members of a separate population.

Old field.—This area is comprised of a field abandoned for approximately 15 years (confirmed by a local resident). In the northern part of the field is a small depression that contains a refuse heap; the heap is bordered by *Salix* sp., *Populus tremuloides,* and *Cornus racemosa.* The southern portion of the field slopes into a hardwood swamp. The soil is primarily sandy loam (Miami loam). Sheet erosion on the slopes has removed most of the top soil leaving a sandy clay.

The plant growth is relatively uniform over most of the field. The vegetation consists primarily of *Poa compressa, Potentilla intermedia, Daucus Carota,* and *Plantago lanceolata.* The surface is partly covered by a moss, *Brachythecium* sp. The eroded sites have a sparse cover while the low places support a more abundant growth.

A blue-grass pasture and a small grass-sedge marsh were near the old field. Both were favorable vole habitats and individuals undoubtedly were able to move back and forth between these sites and the field.

Marsh.—This area is for the most part a rather typical marsh. The dominant plants are sedges and grasses. One portion contains a considerable amount of *Solidago* sp. and *Aster* sp. In general the surface is low with the water table only a few centimeters beneath. During the wet season, water stands over most of the area. The soil throughout is typical of marshes (Dansereau, 1957); it contains much fibrous, peaty humus and a moderate amount of mineral matter. As indicated above, the soil moisture is high even when it is not inundated — being nearly saturated during the driest months. The sedges and grasses grow from small hummocks 5 to 10 centimeters in diameter. Each hummock rises 5 to 10 centimeters above the surface. The spaces between the hummocks are usually free of living vegetation. During the winter the dead vegetation falls over and forms a low canopy. Decaying vegetation also falls between the hummocks to form a tangled mat that covers the surface. In the summer the grasses and sedges completely cover the surface.

For more complete descriptions of the areas (including the species of plants present) as well as the adjoining habitats, see Getz (1959). The marsh is the more favorable *Microtus* habitat. The more abundant growth of grass-like vegetation (an average of 325 grams per square meter in the marsh compared with 65 in the old field), as well as the moist soil, results in a higher humidity and more moderate temperatures in the marsh than in the old field. Both of these conditions appear to be favorable for voles. Similarly the larger amount of vegetation in the marsh offers a greater available food supply as well as more protection from predators, especially hawks and owls.

METHODS

The two areas were marked off in a grid pattern with a 12-meter interval. The entire old field was included in the study area while only that part of the marsh feasible to trap was included. The estimated area of each was 2.5 hectares for the old field and 3.6 hectares for the marsh. Where no natural boundaries occurred in the marsh, the study area was assumed to extend out one-half the average diameter of the home range of *M. pennsylvanicus* as determined from the trapping data, or 18 meters beyond the outer row of traps. The old field contained natural boundaries around almost the entire area. The marsh contained natural boundaries around two-thirds of the area.

A trapping period of five nights was employed throughout the study with the two areas being trapped once each month (for exact dates of trapping see Getz, *op. cit.*). Because of the size of the marsh study area (228 stations), two trapping periods were required to cover all stations (133 were trapped the first period). For the first four days of a period the traps were checked twice a day, once at 0800 to 1100 and again from 1600 to 1800 (the exact times depended on the time of sunrise and sunset). On the fifth day they were checked only in the morning; they were then picked up and moved in preparation for the next trapping period. The period of the study was September, 1957, through September, 1958.

Wooden multiple-catch traps of the type described by Burt (1940) were employed throughout the study. These proved effective with only a few voles escaping or chewing out. Bait consisted of equal amounts of sunflower seeds and commercial chicken scratch. No prebaiting as such was employed. Traps normally were placed at the stations at least a day in advance of a trapping period. Since most of the traps contained some bait from the previous period, this may have served as a type of prebaiting. A small piece of cotton was provided in each trap from November through May to serve as insulation and to absorb moisture (urine, rain, or dew). Mortality in the traps was low. Of the 1,128 individuals captured a total of 6,412 times, only 74 (6.6%) died in the traps. Individuals were marked by toe clipping in a manner similar to that described by Gunderson (1950). No more than two toes were clipped on any one foot. No anesthesia was used. Only three instances of infection caused by the clipping were noted and one of these individuals was taken several months later. I do not believe that such clipping resulted in any appreciable mortality.

Some difficulty was experienced in the marsh where traps were disturbed by raccoons, opossums, weasels, and rabbits. Most of these animals had to be removed from the area by trapping if the study was to continue. Although the removal of the weasels (seven individuals) which were feeding on the voles (from examination of stomach contents) undoubtedly affected the population to some extent, no obvious effects were noted.

Field data (area, station number, species, individual number, sex, reproductive condition, and age class) were recorded on prepared forms. The capture data were transcribed onto 3 by 5 file cards (one for each individual).

POPULATION DENSITY

Densities of *M. pennsylvanicus* populations have been recorded by Hamilton (1940), Blair (1940), Bole (1939), and Townsend (1935). Depending upon the habitat and the method of sampling, these have varied from 0 to 92 per hectare. Hamilton (1940) has published data concerning population densities during various stages of the population cycle.

Population densities were computed for both areas based on the number of voles captured or known to be present each month. Some marked individuals not caught during one month but captured in subsequent months were considered to have been present during the months they were not captured.

The population density of the old field was at all times much less than that of the marsh (Fig. 1). At its highest point the population density of the old field was just equal to that of the marsh at its lowest point. This difference in density has been attributed to differences in the amount of graminoid vegetation present in each area (Getz, in press).

The marsh displayed greater monthly fluctuations in population density (extremes of 18 and 63 per hectare) than did the old field (6 to 18 per hectare). The more favorable conditions in the marsh allowed for a greater build-up in population sizes during the breeding seasons. The lesser vegetation cover in the old field resulted in more extreme temperatures and moisture conditions (Getz, *op. cit.*). This probably resulted in the movement of several individuals out of the old field

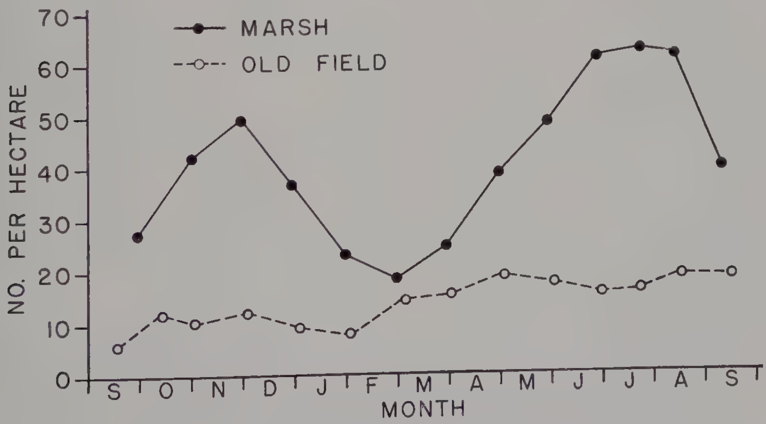

Fig. 1.—Population densities of *Microtus pennsylvanicus* in the two study areas.

and into nearby areas that supported more dense stands of vegetation. Trapping (during the July census) in a portion of the small marsh adjoining part of the old field resulted in the capture of one individual (out of seven captured) that had moved there from the old field. The lesser cover would also make the voles more susceptible to predation than in the marsh. Data concerning recaptures of individuals from month to month show that during the early summer and in the fall a greater percentage of the population was lost from the old field than from the marsh (Fig. 2). The peaks of the population, therefore, were suppressed somewhat in the old field so that the relative amount of fluctuation of population density was less than that of the marsh.

The data from the marsh indicate two definite peaks and two troughs of density during the year. Those from the old field indicate approximately the same characteristics although the peaks are somewhat smoothed and a drop in the density is not indicated by the September, 1958 data. The two peaks of population density result from the two main breeding seasons, spring and fall (see below). Breeding decreases during the summer resulting in a drop in the population density in the late summer or early fall. Owing to the relatively short life span of *M. pennsylvanicus,* few adult individuals survive from the spring to the fall breeding season. Also an increased loss of animals from the populations in late summer and during the winter (Fig. 2) further accentuates the depth of the troughs (especially in the marsh). From examination of the data, mortality, rather than movement, appears to be the major cause of loss of individuals.

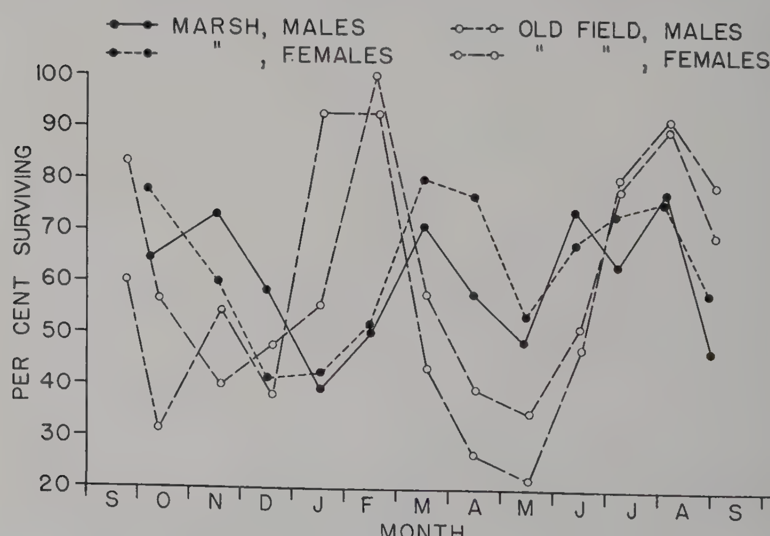

Fig. 2.—Percentage of the population present one month that survived until the next month.

In general the changes in population density in the old field were approximately 2 to 3 months ahead of those of the marsh. The earlier peak density in the old field in the spring results from an earlier breeding season in this area than in the marsh.

Since the study encompassed only one year, no evidence of a cycle was obtained. The population densities may have been slightly higher in September, 1958, than in September, 1957, but do not appear to be different enough to indicate an upward trend in the population levels. As stated above, the fluctuations in density that did occur were attributed to the limited periods of reproduction and are not indicative of a cyclic fluctuation.

SURVIVAL

Loss of individuals from a study area can occur in two ways, death of the individual or movement off the area. Blair (1948) stated that emigration accounted for only 10 per cent of the losses from a population. From data on movement of individuals this appears to be approximately true of the areas of the present study. Deaths can be caused by various factors, but losses to predators probably account for the vast majority of them (Blair, *op. cit.*).

Since data were obtained for a period of only one year, the information concerning survival of individuals is limited. It has been possible, however, to obtain a fairly clear indication of the length of survival in the two areas and to make comparisons. Two methods of determining survival were utilized. The first method was based on the estimated number of young produced by the population each month. The number of pregnant and lactating females observed each month was multiplied by the average number of offspring per litter. Hamilton (1941) and Bailey (1924) found the average number of young per litter of *M. pennsylvanicus* to be five. Counts of the number of young in the litters born in the traps and the number of embryos in those pregnant females that died in the traps indicate a similar mean for the populations here studied. Only those females definitely pregnant (and thus close to parturition) were recorded. It is assumed, therefore, that owing to the rapid development of voles (Hamilton, *op. cit.;* Bailey, *op. cit.*) the offspring of these individuals would be captured as subadults the next trapping period. Those individuals not yet weaned were not normally taken during that month and still were "subadults" the next trapping period. The subadults actually captured in a given month were then considered to be the survivors of those born of females pregnant the last trapping period or weaned since then. The percentages of survival in subsequent months, based on the estimated number born, were computed to determine a survival curve for *M. pennsylvanicus.* Owing to the age of the individuals and their small size, I believe that losses during the first month of life resulted primarily from deaths (especially to predators) rather than from movement off the area.

The second method recorded the length of time each individual remained on a study area after it was first captured. Thus, the per-

centage of those surviving each successive month was computed, based on the number captured for the first time a given month. In other words, of the individuals first captured in October, November, December, etc., the number surviving for each succeeding month was determined to obtain survival curves for each sex as well as for those first captured as adults or subadults.

Since there were relatively few captures of subadults (especially from the old field) the data from both areas and both sexes were combined to determine survivals from the estimated births. As can be seen (Fig. 3), mortality was far greater during the first month of life than at any other time. In both the marsh and the old field only 12 per cent of those estimated to have been born were actually captured. The semi-log plot shows that the curve of survival for the remaining months approaches a straight line, an indication of a constant specific rate of survival after the first month of life. The average life span of *M. pennsylvanicus* as indicated by this data is 0.7 months.

The high mortality rate most likely results from predation, probably by garter snakes. *Thamnophis sirtalis* and *T. sauritus* were both abundant in the area. Time was not available to make a food habit

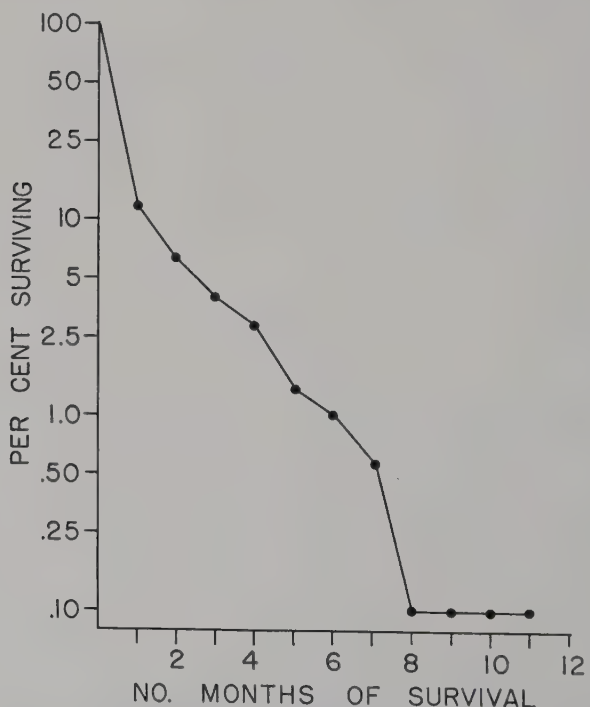

Fig. 3.—Semi-log plot of the survival curve from birth. Based on an estimated 1665 births.

TABLE I.—Mean survival of *Microtus pennsylvanicus* in the study areas (only those individuals first captured October, 1957, through March, 1958, are included)

Area	Sex	Age at first capture	No. of individuals	Mean survival (months)	SD
Marsh	Male	Adult	126	2.2	1.8
Marsh	Male	Subadult	21	2.7	2.0
Marsh	Female	Adult	133	2.1	1.8
Marsh	Female	Subadult	40	2.1	2.0
Old field	Male	Adult	49	1.6	1.1
Old field	Male	Subadult	21	1.9	1.7
Old field	Female	Adult	52	1.9	1.3
Old field	Female	Subadult	10	1.3	0.7

study of these species to confirm this assumption. Hamilton (1951) found that these snakes fed upon voles. Young voles, still in the nest, would be especially susceptible to predation by snakes.

No difference in the survival of either sex during the first month was found. Assuming the sex ratio to be equal at birth, the survival

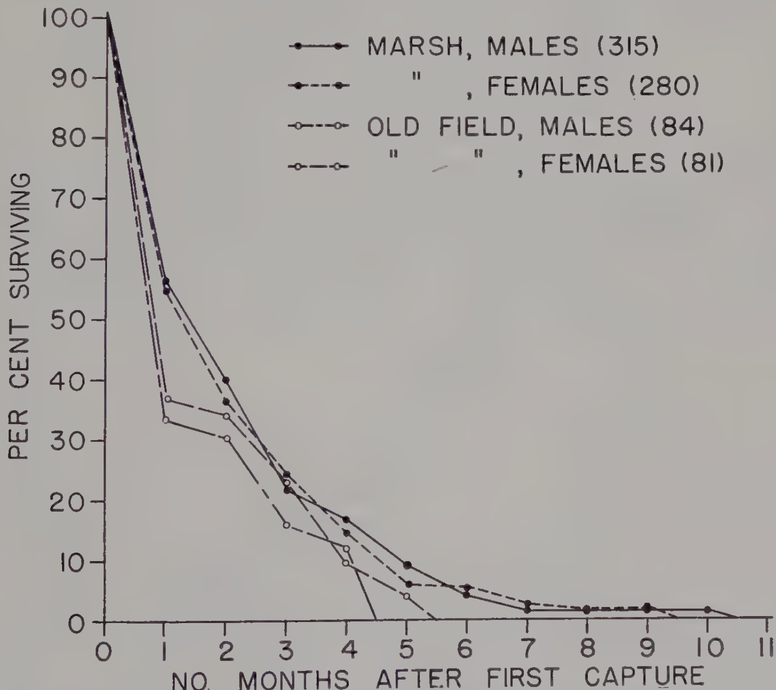

Fig. 4.—Survival of individuals first caught as adults. Figures in parentheses indicate the number of individuals involved.

of both sexes was approximately 12 per cent. The sex ratio of the individuals captured as subadults was 100 males to 101 females.

Figures 4 and 5 and Table I give the survival of individuals after their first capture. Blair (1948) found that the average time the individuals remained in his study areas was 4.23 ± .22 months. My data indicate the time is approximately one half that recorded by him. Since his trapping periods were approximately three months apart, the resulting averages indicate most individuals to have been taken during only one trapping period. Blair's results, therefore, appear to be related more to the interval between trapping periods than to the actual survival of the voles on his study areas. The longest survival recorded in my study was 11 months (two individuals). Hamilton (1941) estimated the maximum longevity of *M. pennsylvanicus* under field conditions at 16 months.

The average survival (based on month of first capture) as well as the survival curves were similar for all the males and females in both areas (Fig. 4 and Table I). The data concerning those first captured as adults in the marsh, when plotted on a semi-log scale,

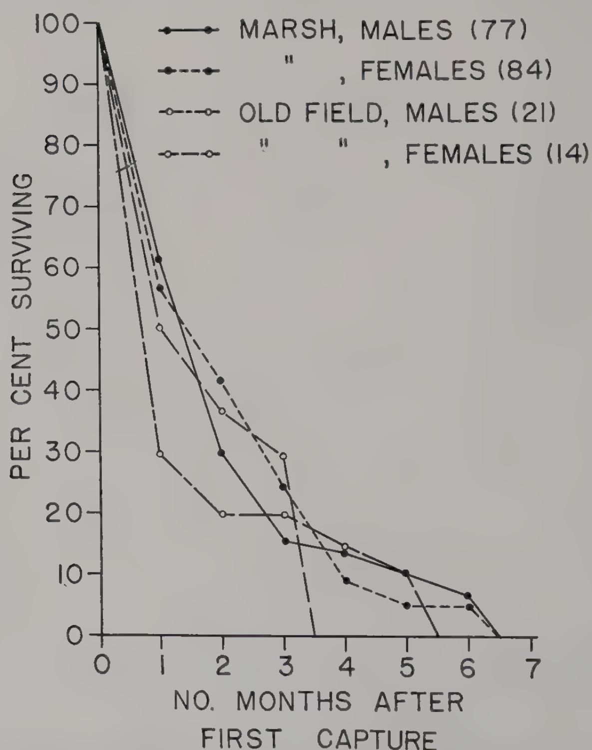

Fig. 5.—Survival of individuals first caught as subadults. Figures in parentheses indicate the number of individuals involved.

approach a straight line. This further indicates a constant specific survival of individuals after the first month of life. Data from the old field do not form a straight line, but fewer records were obtained and the data may not be significant. The survival of both sexes in the marsh was longer than, although not significantly different from, survival in the old field. As stated above, shorter survival time in the old field is attributed to the lesser amount of vegetation that resulted in less favorable moisture and temperature conditions as well as in greater predation.

Comparisons of the population losses between trapping periods in the marsh indicate a slightly greater loss during the winter months than at other seasons (Fig. 2). There is also a decrease in survival during the breeding season and another drop in August. The curves for the males and females show similar trends. The spring and summer data from the old field agree in general with those from the marsh. Those from the fall and winter differ somewhat, especially those for the December-January and January-February periods. The survival in the old field for both sexes during these latter periods is higher than at any other time during the year. Only a few individuals were present during these months and these data may not be significant. Owing to the harsh environmental conditions in the old field during the winter, it does not seem probable that survival would normally be as high as the few data obtained would indicate.

POPULATION STRUCTURE

The sex ratio based on all individuals captured during the study was approximately equal. The average monthly percentages of males were 49.8 ± 5.9 for the marsh and 49.9 ± 8.1 for the old field. The greatest percentage of males in the marsh (60) occurred in the month of March while the highest in the old field (70%) occurred in February (Fig. 6). A greater amount of movement of the males in the marsh during March apparently results in the higher percentage of

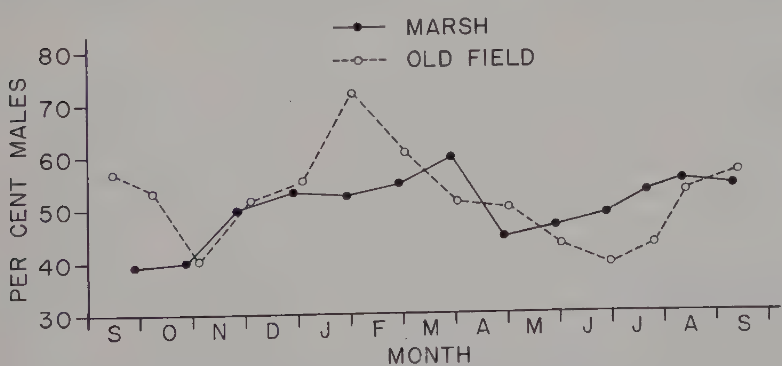

Fig. 6.—Monthly variation in the percentage of males (all age classes) in the population.

this sex in the population. The same appears to be true of the old field, but the number of individuals involved was not sufficient to determine this for certain.

Two age classes, subadult and adult, were distinguished by size and pelage, Because of two definite breeding seasons, the subadults made up an important part of the total population for only a portion of the year (Fig. 7). The difference in the breeding seasons in the old field and marsh resulted in differences in the percentage of subadults in the two areas for given months.

REPRODUCTION

The reproductive status of the adult females was determined by gentle palpation of the region of the uterus. Undoubtedly individuals in early stages of pregnancy were missed, but the limited time available for handling individuals did not permit a more thorough examination. In addition, a check was made of the vulva to see if it was open, an indication that the individual was in breeding condition.

Reproduction was limited primarily to two periods in both areas, spring and fall. This was reflected in the number of pregnant females and the appearance of young (Figs. 7 and 8). Gunderson (1950), in Minnesota, likewise found breeding to occur primarily in spring and fall. Extremely low temperatures in the winter and high temperatures in the summer probably result in unfavorable conditions for breeding. Hamilton (1941) has given evidence to support the relationship between temperature extremes and cessation of reproduction in *M. pennsylvanicus*. Temperature data for the two areas are given by Getz (in Press).

The breeding seasons in both areas are approximately the same except that in the old field the spring breeding commences earlier and ends earlier than in the marsh (Fig. 8). The spacing of the trapping periods in the two areas tends to overemphasize the later commencement of breeding in the marsh. The old field was trapped immediately after the marsh, but there was an interval of one week before the marsh was trapped again. Since the April trapping of the old field immediately followed the March trapping of the marsh, and no indication of any pregnant females was found in the marsh at that time, it is evident that breeding commenced earlier in the old field. Examination of the vulvae revealed none to be open in females in the marsh in February. Twenty per cent of the females in the old field had open vulvae during the March trapping (which occurred immediately after the February trapping of the marsh). A newly born individual was found dead in a path in the old field during the March trapping period. This further indicates that breeding commenced very early in this area. It is also obvious that breeding decreased sooner in the old field than in the marsh (Fig. 8).

The most plausible explanation for the earlier breeding in the old field is that the grass began growing earlier here than in the marsh. During the March trapping of the marsh, the surface was almost

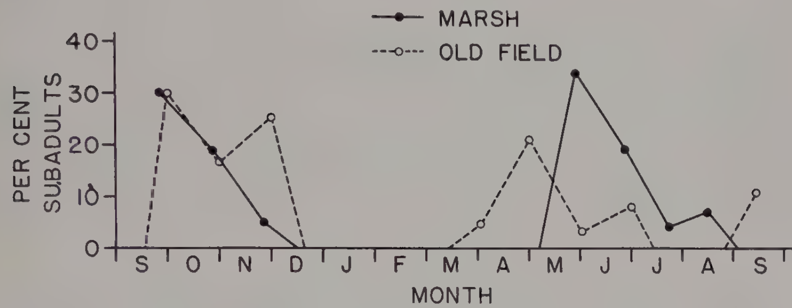

Fig. 7.—Monthly variation in the percentage of subadults in the two populations.

completely covered by ice and the vegetation had not begun to grow. The vegetation (particularly the grass) in the old field, on the other hand, had grown so that the green shoots were eight to ten centimeters tall by the time of the April trapping (immediately after the March trapping of the marsh). By the April trapping period in the marsh, the vegetation in this area had begun growing (25 to 30 centimeters tall) and reproduction of the voles was approaching its peak. Hoffman (1958) found that breeding in *Microtus californicus* and *M. montanus* is correlated with the growth of green vegetation.

The earlier decrease in breeding in the old field evidently is related to temperature and humidity conditions. Owing to the sparse cover in this area temperatures were rather high during the summer. Soil moisture became very low; probably air humidities were also low near the surface of the soil during these months. This contrasted with conditions in the marsh where the dense vegetation resulted in more moderate air temperatures and higher soil moistures (thus higher air humidity). That reproduction ceased completely in the old field while not ceasing entirely in the marsh (although dropping consider-

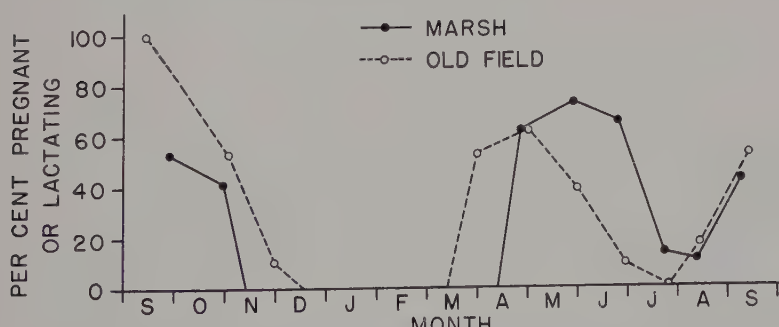

Fig. 8.—Monthly variation in the percentage of pregnant or lactating females in the two populations.

ably) further indicates the importance of the influence of temperature and moisture conditions upon reproduction.

The resumption of breeding in August and September is not explained on the basis of physical factors. Rainfall had not increased, nor had temperatures dropped until the last day of trapping in the old field (and after the study was completed). The percentages of pregnant females were approximately the same in both areas during August and September so perhaps some non-environmental "trigger" was involved.

Conclusions

The data from the two study areas in general follow the same trends. The differences that do occur, especially those concerning population densities, survival, and breeding apparently, result from the environmental differences in the two areas. The amount of cover with its modifying influence upon temperature and moisture conditions as well as protection from predators appears to control the time of occurrence of the various population phenomena.

As in many other species of small mammals, survival during the first month of life is very low for *M. pennsylvanicus.* After the first month there is no indication of senescence, that is to say, deaths occur at a constant rate regardless of the age of the animals. The survival data indicate that the approximate maximum age attained by *M. pennsylvanicus* in the wild is 11 to 12 months with an average of less than one month. Approximately 25 per cent of the adult individuals survive the three months between the spring and fall breeding seasons and only six per cent survive the five months between cessation of breeding in the fall and its resumption in the spring. *M. pennsylvanicus,* therefore, is essentially a semi-annual species in southern Michigan.

Summary

Two populations of the vole, *Microtus pennsylvanicus* in southern Michigan were live-trapped at monthly intervals for 13 months. One population occurred in a 2.5 hectare abandoned field ("old field"). The other occurred in a grass-sedge marsh 630 meters from the first. The study area in the marsh comprised 3.6 hectares. The marsh was the more favorable vole habitat.

The population densities of the marsh were always greater than those of the old field. The densities in the marsh varied from 18 to 63 individuals per hectare while those of the old field varied from 6 to 18 per hectare. Two peaks (spring and fall) and two troughs (late summer and winter) of density occurred. These resulted from the restriction of breeding to two main periods, spring and fall. The short life span of *M. pennsylvanicus* (0.7 months) resulted in the loss of most of the population between the breeding seasons. A greater loss of individuals from the populations in winter further accentuated the fluctuations.

The greatest mortality occurred during the first month of life (88%). After that there is a constant specific rate of survival. The average length of time the adult individuals remained on the study

areas was approximately two months. The length of survival was somewhat less in the old field than in the marsh. This was attributed to the less favorable conditions of cover, food, moisture, and temperature in the old field that resulted in more emigration and/or a higher loss to predators. No significant difference was observed between the length of survival of males and females in either area.

Reproduction occurred primarily during two seasons, spring and fall. Reproduction began one month earlier in the old field than in the marsh, a result of an earlier start in the growth of the vegetation in the old field. Breeding almost completely ceased during the summer, resuming at approximately the same time (September) in both areas. The reason for the resumption of breeding in the fall did not appear to be correlated to any environmental factor.

Owing to the relatively short life span, *M. pennsylvanicus* is essentially a semi-annual species in southern Michigan.

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An Ecological Study of Benthic Organisms in Three Illinois River Flood Plain Lakes

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This paper is concerned largely with the dynamics and changes in the benthic populations of three flood plain lakes located along the Illinois River near Havana, Illinois. For a number of years these lakes have been affected by sewage and industrial pollution from the Illinois River. Prior to 1926 Richardson (1921a,b; 1925a,b; and 1928) studied the bottom fauna of the Illinois River and certain of its flood plain lakes. Two of the lakes included in Richardson's work were studied during the present investigation.

Both the human population and industries along the Illinois River have nearly doubled since Richardson's (*op. cit.*) studies were made. In 1913-14 Richardson (1921a) found that benthic organisms in the river and lakes in the vicinity of Havana (Fig. 1) were those normally found in relatively clean waters. Between 1917 and 1920 there was an increase in pollution in the river which wiped out most of the former clean water species in the Havana area (Richardson, 1925b and 1928). By 1925 there had been only a mild improvement in sanitary conditions of the river. Improvements apparently have occurred in the sanitary conditions of the river since 1925. Sewage disposal plants built after 1925 in most urban areas along the river above Havana have helped to reduce pollution in the river. In the 1930's several large navigation dams were constructed on the river, and they have tended to reduce the rate of flow of the river, thereby, allowing more time for a natural breakdown of certain pollutants. However, pollution in the form of silt has greatly increased in the river and its flood plain lakes since the time Richardson made his investigations.

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METHODS AND MATERIALS

The present study was started in July, 1952 and concluded in April, 1958. The bottom fauna samples were all taken in mud with a 6 x 6-inch Ekman dredge; dredgings were washed through a No. 30 sieve and the collected organisms preserved in formalin. Individual counts were made of the preserved organisms. For determining the numbers of Oligochaeta the anterior ends were counted. The few specimens of Crustaceans, Pelecypoda (other than Sphaeriidae), Corixidae, Nematoda, and Hydracarina taken in the collections were considered as accidental and were therefore excluded from the study. Wet weights of organisms were recorded to the nearest 0.01 gram. A sample of Sphaeriidae and Gastropoda weights with and without shells was made to determine a factor for calculating molluscan weights without shells. Shell weights were deducted from the molluscan weights by multiplying the wet weights of Sphaeriidae by 0.60 and of Gastropoda by 0.35. Weights of Trichoptera, Diptera and Oligochaeta were determined after the cases and/or mud were removed.

A total of 363 dredgings were made: 57 in Lake Matanzas, 130 in Quiver Lake, and 176 in Lake Chautauqua. Because of the relatively small number of samples taken, the samples for each sampling period from all stations in each lake were combined.

TABLE I.—Summary of chemical analyses of monthly water samples from Lake Matanzas, Lake Chautauqua and Quiver Lake, Illinois (June, 1953- May, 1954)

Symbols	Lake Matanzas Range (ppm or pH units)	Lake Matanzas Mean	Lake Chautauqua Range (ppm or pH units)	Lake Chautauqua Mean	Quiver Lake Range (ppm or pH units)	Quiver Lake Mean
pH	7.6- 8.6	8.3	7.8- 8.6	8.2	7.8- 8.4	8.0
Fe	0.4- 2.5	1.3	0.2- 7.6	1.8	0.3- 11.3	2.6
PO_4	0.0- 0.5	0.2	0.1- 1.2	0.4	0.1- 1.0	0.4
SiO_2	0.6- 17.7	7.1	0.7- 15.8	5.7	8.1- 17.0	12.7
CO_2	1.0- 7.7	2.4	0.8- 9.0	3.0	2.0- 16.0	6.4
Cl	3.0- 13.0	7.9	7.0- 15.0	10.5	4.0- 15.0	8.9
SO_4	40.3- 76.7	51.4	50.4- 93.4	68.8	39.1- 91.3	60.8
NO_3	0.0- 4.5	2.1	0.0- 4.1	1.1	2.3- 10.4	6.4
NH_4	0.3- 0.7	0.4	0.1- 0.5	0.3	0.0- 0.5	0.2
Ca	36.5- 53.5	45.2	43.6- 57.0	49.2	55.3- 76.0	62.6
Mg	14.6- 20.0	17.2	16.9- 24.4	21.1	19.1- 26.2	20.6
Na	1.8- 12.0	7.9	4.1- 12.2	8.5	1.4- 14.6	8.4
Alkalinity (as $CaCO_3$)	96.0-164.0	135.3	124.0-160.0	141.7	148.0-220.0	186.0
Hardness (as $CaCO_3$)	157.0-216.0	183.8	179.0-243.0	209.8	217.0-298.0	248.3

Representative organisms from various dredgings were submitted to specialists for identification. The remainder of the identifications were made by us on the basis of the determinations of the specialists.

Test netting for black crappies, *Pomoxis nigromaculatus,* was done with 1-inch wing nets (with leads) as described by Starrett and McNeil (1952) and Starrett and Barnickol (1955).

Water samples were collected at monthly intervals between June, 1953 and May, 1954 from each lake. The water samples were delivered within 24 hours to the Water Survey Division Laboratory at Champaign, Illinois, for chemical determinations. The pH of each water sample was determined in the field.

Results of chemical analyses are summarized in Table I. Chemical characteristics for the three lakes were quite similar, except that car-

Fig. 1.—Map showing the Illinois River and locations of Lake Chautauqua, Quiver Lake and Lake Matanzas, Illinois.

bon dioxide, calcium, alkalinity and hardness were slightly higher in Quiver Lake than in the other two lakes. The analyses indicated that all three lakes were rich in nutrients.

A total of 24 water samples for bacteriological analysis was taken during 4 collecting periods from each lake between August and December, 1953. Lake levels remained low during this period. Samples were taken from both the surface and near the bottom of the lakes. They were iced immediately and delivered within two hours for analysis to the Division of Laboratories of the Illinois Department of Public Health at Springfield, Illinois. The analyses are discussed later in this paper. MPN refers to the most probable number of organisms per 100 ml (Hoskins, 1934).

DESCRIPTIONS OF LAKES AND SAMPLING STATIONS

The three lakes studied in this investigation are located in Mason County, Illinois, (Fig. 1) in the flood plain of the Illinois River, and are flooded periodically by the river. Most of the lake bottoms are covered with a layer of loose sediment, mainly deposited since the early 1930's from silt-laden flood waters. The lakes all have narrow-sandy beaches along their bluff-side shores. Seepage of effluents from septic tanks and privies at cottage sites along the bluffs overlooking the lakes provide a source of minor pollution in the lakes.

LAKE MATANZAS

Lake Matanzas covers about 347 acres at normal summer water levels and is 8.5 to 9.0 feet deep. During low river stages the lake is separated from the river by a low head dam and natural river em-

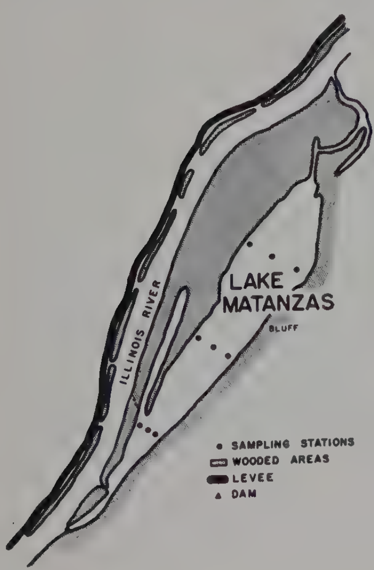

Fig. 2.—Map of Lake Matanzas, Illinois, showing the nine sampling stations used in the study and the site of the lake with reference to the Illinois River.

bankments (Fig. 2). The water level of the lake is raised once or twice a year by flood waters of the Illinois River. Submergent aquatic vegetation was absent from the lake; however, vegetation formerly flourished in the lake (Richardson, 1921a). The effects of turbidity upon aquatic vegetation in an Illinois River flood plain lake have been discussed by Jackson and Starrett (1959).

The abundant fishes in Lake Matanzas are: bluegill (*Lepomis macrochirus*), black crappie, white crappie (*Pomoxis annularis*), gizzard shad (*Dorosoma cepedianum*), bigmouth buffalo (*Ictiobus cyprinellus*), carp (*Cyprinus carpio*), and spottail shiner (*Notropis hudsonius*).

At Lake Matanzas the bacterial coliform counts ranged from <23 to 620 MPN/100 ml and the enterococcus counts ranged from <2.3 to 130 MPN/100 ml.

The nine sampling stations in Lake Matanzas were located on three transects as indicated in Figure 2. The bottom fauna samples were taken at the various depths and seasons given in Table II. Most of the samples at Lake Matanzas were taken during the month of October.

QUIVER LAKE

Quiver Lake differed from the other two lakes in that it was connected at all times with the Illinois River (Figs. 3 and 4). At low river stages, the river flows only through the extreme lower end of the lake, but at a river stage of about 8.0 feet at Havana (14.0 ft. flood stage) a portion of the river flows through the entire lake. Current was seldom perceptible in Lake Matanzas or Lake Chautauqua, even during periods of high river stages.

Quiver Lake covers about 408 acres at normal summer water levels. For purposes of this study, Quiver Lake was arbitrarily separated into three areas (Fig. 4). Most of Upper Quiver Lake tended to become dry during periods of low river stages; Middle Quiver Lake did not have a current present when the river stage was below 8.0 feet; and Lower Quiver Lake was actually a part of the river and some current was always present. Benthic studies of Quiver Lake were conducted primarily on Middle Quiver Lake.

At low river stages the maximum depth of Middle Quiver Lake was 6.5 to 7.0 feet. In 1914 and 1915 when Richardson (1921a) studied Quiver Lake the maximum depth was 12.0 feet at low water stages. Much of the lake has silted-in since the time of Richardson, and in the 1920's more water was diverted from Lake Michigan into the river than at present. Formerly, higher aquatic plants abounded in Quiver Lake (Hart, 1895; Kofoid, 1903; and Richardson, 1921a); whereas, at the time of the present investigation vegetation was completely absent from the lake. In 1953 and 1954, turbidity in Quiver Lake ranged from 25 to 775 ppm. (Jackson, 1954). Jackson (*op. cit.*) detected the presence of a temporary thermocline in Middle Quiver Lake during a period of warm weather in the summer of 1953.

The abundant fishes in Quiver Lake are: gizzard shad, black

crappie, bullheads (*Ictalurus* spp.), bigmouth buffalo, carp, and emerald shiner (*Notropis atherinoides*).

The coliform counts from Middle Quiver Lake in 1953 ranged from 230 to 24,000 MPN/100 ml and the enterococcus counts ranged from <2.3 to 620 MPN/100 ml.

Six sampling stations located on two transects were used on Middle Quiver Lake (Fig. 4). On Upper Quiver Lake three sampling stations were used, and on Lower Quiver Lake four sampling stations

Fig. 3.—An aerial photograph, taken in 1954, of Quiver Lake and the lower part of Lake Chautauqua, Illinois. During a period of high water the two lakes are connected. The photograph depicts the relationship between the Illinois River and Quiver Lake at a moderately high river stage.

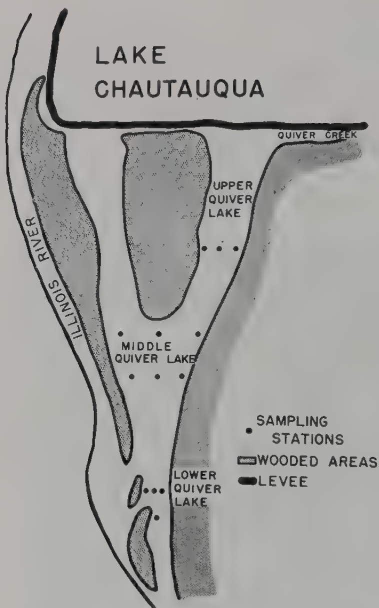

Fig. 4.—Map of Quiver Lake, Illinois, showing the sampling stations used during the investigation. Quiver Creek shown on the map flows directly into the river at low river stages.

were used (Fig. 4). The water depths at the time dredgings were made are given in Table III.

Lake Chautauqua

At normal lake stage (435.0 ft. mean sea level) Lake Chautauqua covers 3,562 acres. The lake is a part of the Chautauqua National Wildlife Refuge and is managed primarily for waterfowl by the U. S. Fish and Wildlife Service. A system of levees with spillways and control gates separate the lake from the Illinois River at normal river stages (Fig. 5). At a river stage of about 12.2 feet at Havana the river enters the lake and this usually occurs once or twice a year.

Most of Lake Chautauqua is between 2 and 3 feet deep at normal lake level and at such a level nearly the entire lake is within the euphotic zone (Jackson and Starrett, 1959). No period of summer stagnation has been known to occur in the lake. Sago pondweed (*Potamogeton pectinatus*) becomes abundant in years when water levels remain low and stable during the growing season. During this investigation pondweed was abundant only in 1953 and 1956. Stall and Melsted (1951) found in 1950 that within a 23.8-year period the storage capacity of Lake Chautauqua had been reduced 18.3 percent by sedimentation. Turbidity of the lake between 1953 and 1956 varied from <25 to 800 ppm (Jackson and Starrett, 1959).

The most abundant fishes in Lake Chautauqua are: gizzard shad, white crappie, black crappie, bluegill, freshwater drum (*Aplodinotus grunniens*), bigmouth buffalo, carp, yellow bass (*Roccus mississippien-*

sis), channel catfish (*Ictalurus punctatus*), emerald shiner, and spot-tail shiner.

Coliform counts at Lake Chautauqua ranged from <23 to 2,400 MPN/100 ml, and enterococcus counts ranged from <2.3 to 6,200 MPN/100 ml.

On Lake Chautauqua benthic samples were taken at 21 sampling stations located on 7 transects established by Stall and Melsted (1951) (Fig. 5). The water depths at which the dredgings were made are summarized in Table IV.

BOTTOM FAUNA

The bottom fauna data presented here are given as standing crops per square foot. No attempt was made to determine the production of benthic organisms in the manner described by Lundbeck (1926), in which he estimated that the annual production in the Plöner See was about three or four times the average summer fauna. The studies of Hayne and Ball (1956) in Michigan indicated that in the presence of fish the average production of bottom fauna fish food during the growing season was about 17 times that of the standing crop. The standing crops given in the present paper are therefore merely only a fraction of the actual production that probably occurred each year in the lakes studied.

The benthic population differed considerably among the three lakes, particularly on a weight basis (Fig. 6 and Table V). The weight of bottom fauna of Middle Quiver Lake was comprised largely of

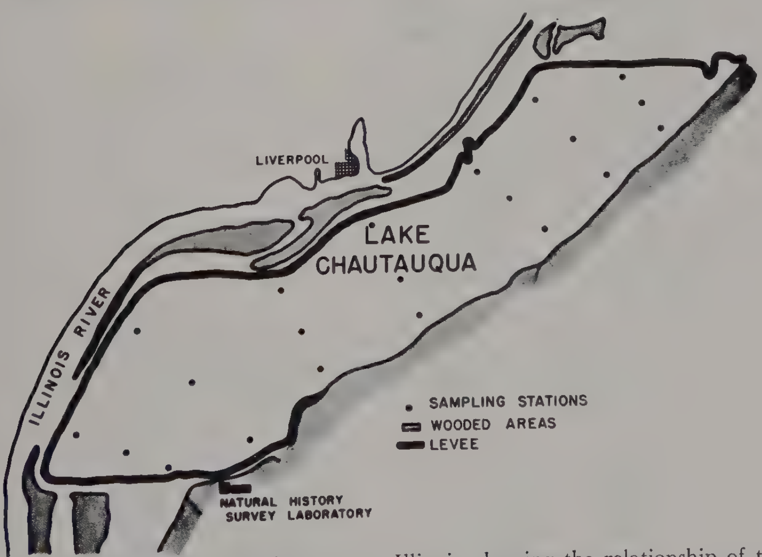

Fig. 5.—Map of Lake Chautauqua, Illinois, showing the relationship of the lake to the Illinois River. The map also shows the locations of the 21 sampling stations used during the study.

mollusca; whereas, in Lake Chautauqua insect larvae predominated. Worms and insect larvae were the important constituents of the bottom fauna in Lake Matanzas. In Lake Chautauqua and Lake Matanzas, mollusca formed only a small part of the total population. On

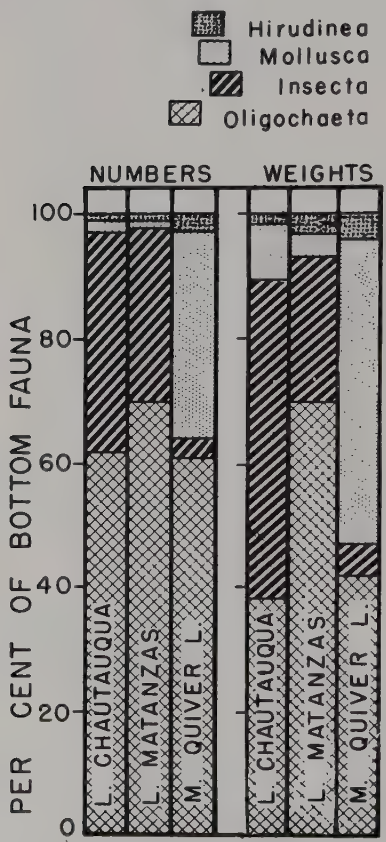

Fig. 6. — Composition of bottom fauna organisms at Lake Chautauqua (1952-56), Lake Matanzas (1952-56) and Middle Quiver Lake (1952-58), Illinois.

TABLE II.—Depths in feet at which bottom fauna samples were taken at Lake Matanzas, Illinois, 1952-56

Season		Range in depth	Mean depth
1952	Fall	1.8- 4.5	3.1
1953	Spring	6.6-10.6	8.8
1953	Summer	3.3- 7.2	5.7
1954	Fall	3.5- 8.5	6.3
1955	Fall	3.5- 8.5	6.3
1956	Fall	3.5- 8.0	6.0

a basis of numbers, worms formed more than 60 per cent of the total benthic organisms collected from all three lakes (Fig. 6).

The average annual standing crops as determined for each lake varied considerably from year to year (Fig. 7). The high standing crop of 14 grams per square foot (excluding shell weights) in 1952 in Middle Quiver Lake was comprised largely of snails and fingernail clams. The standing crop of mollusca in that lake dropped from 10.1 grams in 1952 to 1.4 grams in 1953. Other than in 1953 the standing crop of organisms at Lake Matanzas remained approximately the same each year. In most years the standing crop of benthic organisms in Lake Chautauqua was nearly double that of Lake Matanzas. The chief difference between those two lakes was in the greater abundance of dipterous larvae that occurred in Lake Chautauqua (Fig. 7).

TABLE III.—Depths in feet at which bottom samples were taken at Quiver Lake, Illinois, 1952-58

Year and name of lake	Range in depth	Mean depth
Upper Quiver Lake		
1952	0.4- 4.1	2.9
1953	1.1- 8.5	5.2
1957	6.0- 9.5	7.9
Middle Quiver Lake		
1952	0.7- 8.9	4.1
1953	1.0-13.3	5.3
1954	1.0-12.5	6.0
1955	3.0- 9.0	4.7
1956	6.5-12.0	8.9
1957	7.5-13.0	9.8
1958	9.0-14.5	11.4
Lower Quiver Lake		
1952	1.3-11.0	6.0
1953	2.0-13.5	7.7
1954	3.5-10.0	6.6

TABLE IV.—Depths in feet at which bottom fauna samples were taken at Lake Chautauqua, Illinois, 1952-56

Season		Range in depth	Mean depth
1952	Summer	1.4-3.8	2.8
1952	Fall	1.4-3.8	2.6
1953	Spring	2.5-5.5	4.2
1953	Summer	1.1-4.1	2.7
1954	Summer	1.5-3.5	2.4
1955	Summer	1.0-3.5	2.1
1956	Summer	1.7-5.1	3.1

The various invertebrate organisms identified from the three lakes are listed below. The classification of Tendipedini used by Townes (1945) was followed in this paper. After each organism listed below is the lake or lakes in which it was collected, with the lakes being designated as: (M) for Lake Matanzas, (Q) for Quiver Lake, and (C) for Lake Chautauqua.

ANNELIDA

OLIGOCHAETA

Limnodrilus spp. (M, Q, & C)
Tubifex sp. (M, Q, & C)
Dero sp. (M, Q, & C)

HIRUDINEA

Helobdella stagnalis (Linn.) (M, Q, & C)
H. elongata (Castle) (M, Q, & C)
H. lineata (Verrill) (Q)
Erpobdella punctata (Leidy) (M & Q)
Glossiphonia complanata (Linn.) (Q)
Placobdella montifera (Moore) (M & Q)
Myzobdella moorei (Meyer) (Q & C)
Actinobdella inequiannulata (Moore) (C)
Dina sp. (Q)

ARTHROPODA

INSECTA

EPHEMEROPTERA

Hexagenia limbata (Serv.) (Q)
Hexagenia sp. (M)
Caenis sp. (C)

ODONATA

Anax sp. (Q)
Ischnura sp. (C)
Enallagma signatum (Hagen) (C)

MEGALOPTERA

Sialis sp. (Q & C)
Chauliodes sp. (Q)

TRICHOPTERA

Oecetis inconspicua (Walker) (Q & C)

COLEOPTERA

Stenelmis sp. (Q)

DIPTERA

Chaoborus punctipennus (Say) (M, Q, & C)
Pentaneura (*Monilis* gp.) sp. (Q)
Pentaneura nr. *decolorata* (Mall.) (Q & C)
Anatopynia sp. (C)
Pelopia sp. (M, Q, & C)
P. nr. *stellata* (Coq.) (Q)
P. sp. B. (Joh.) (C)
Procladius sp. (M, Q, & C)
P. nr. *bellus* Loew (C)
P. nr. *choreus* Meigen (C)
P. choreus Meigen (C)
Coelotanypus concinnus (Coq.) (M, Q, & C)
C. nr. *concinnus* (Coq.) (C)
Cricotopus nr. *fugax* (Joh.) (C)
Hydrobaenus sp. (Q)
Tendipedini (tribe) (C)
Polypedilum sp. (M)
Cryptochironomus digitatus (Mall.) (M, Q, & C)
C. nr. *digitatus* (Mall.) (M, Q, & C)
C. sp. (*fulvus* (Joh.) ?) (C)
Tendipes sp. (M, Q, & C)
T. plumosus (Linn.) (M & C)
T. nr. *plumosus* (Linn.) (M, Q, & C)
T. staegeri (Lund.) (C)
Glyptotendipes sp. (C)
G. sp. prob. *labiferus* (Say) (C)
Palpomyia sp. (M, Q, & C)
P. nr. *tibialis* (Meigen) (M & C)

MOLLUSCA

GASTROPODA

Valvata tricarinata (Say) (Q & C)
V. lewisi (Cur.) (Q)
Viviparus contectoides (Bin.) (Q)
V. intertextus illinoisensis (Baker) (Q)
Lioplax subcarinata (Say) (Q)
Campeloma decisum (Say) (Q)
C. integrum (Say) (Q)
C. rufum (Hald.) (Q)
Amnicola limosa (Say) (Q)
Cincinnatia emarginata (Küst.) (Q)
Pleurocera acuta Raf. (Q)

SPHAERIIDAE

Sphaerium sp. (M, Q, & C)
Musculium sp. (M, Q, & C)
Pisidium sp. (M, Q, & C)

In the following sections the abundance and ecological relationships of the various organisms are discussed. The groupings used do not necessarily follow the usual phylogenetic order but have been so arranged to facilitate presentation of the material in a coherent manner.

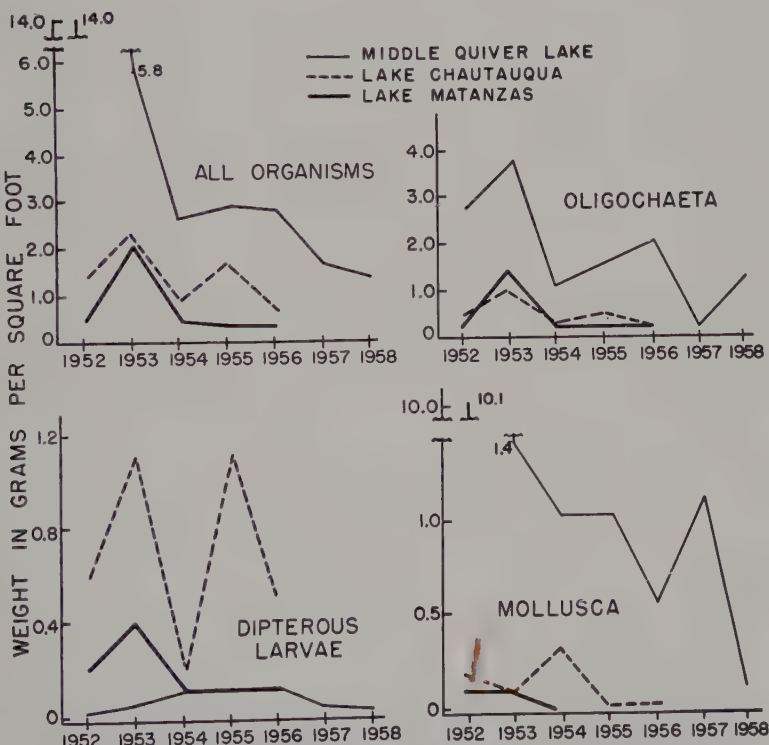

Fig. 7.—Annual fluctuations of standing crops of various benthic organisms at Lake Chautauqua, Lake Matanzas and Middle Quiver Lake, Illinois.

TABLE V.—Average numbers and wet weights of bottom organisms per square foot at Lake Matanzas, Middle Quiver Lake, and Lake Chautauqua, Illinois

Organisms	Lake Matanzas[1]		Middle Quiver Lake[2]		Lake Chautauqua[1]	
	Numbers	Weight in grams	Numbers	Weight in grams	Numbers	Weight in grams
Oligochaeta	348 (86 to 1,223)[3]	0.62 (0.17 to 1.97)	675 (171 to 1,524)	1.87 (0.34 to 3.83)	547 (129 to 1,303)	0.58 (0.17 to 1.09)
Hirundinea	1 (0 to 7)	0.03 (0.00 to 0.15)	25 (0 to 134)	0.18 (0.00 to 0.84)	4 (0 to 7)	0.02 (0.00 to 0.05)
Insecta	138 (79 to 310)	0.21 (0.09 to 0.54)	33 (4 to 61)	0.22 (0.01 to 0.46)	316 (160 to 528)	0.76 (0.26 to 1.49)
Mollusca	8 (0 to 20)	0.05 (0.00 to 0.15)	375 (2 to 2,410)	4.79 (0.19 to 20.77)	19 (0 to 41)	0.23 (0.00 to 0.52)
Total (Shell weight included)	495 (182 to 1,560)	0.91 (0.26 to 2.81)	1,108 (249 to 4,086)	7.06 (1.44 to 24.71)	886 (350 to 1,670)	1.59 (0.63 to 2.69)
Total (Shell weight excluded)	—	0.90	—	4.44	—	1.50

[1] 1952-56.

[2] 1952-58.

[3] Range.

OLIGOCHAETA: — Most of the worms taken in the benthic collections from all three lakes were species of the genus *Limnodrilus*. The abundance of worms (largely Tubificidae) (Table V) in the lakes probably reflected the richness of organic substances found in the lake bottoms. Soil analyses made from samples collected from the bottom of Lake Chautauqua indicated that the sediment deposits from that lake were quite high in fertility (Stall and Melsted, 1951). Soil analyses were not available for the other two lakes studied.

The abundance of worms in the lakes varied from year to year (Fig. 7). In 1953 worms were more abundant in all three lakes than in any other year of the study. Water levels were low in 1953 and such conditions possibly favored the development of large worm populations. Again in 1956 water levels were low, and the worm population in Middle Quiver Lake was higher than for any other time between 1954 and 1958, although in Lake Chautauqua and Lake Matanzas worm populations did not increase in size in 1956 (Fig. 7).

In 1953 the standing crop of worms on the cottage side (bluff side) of Quiver Lake was 0.04 grams per square foot, whereas in the middle and river side of the lake the standing crops of worms ranged from 5.27 to 6.19 grams per square foot. The coliform bacterial count in that year on the cottage side of the lake varied from 230 to 24,000 MPN/100 ml and elsewhere in the lake the count ranged from only 94 to 6,200 MPN/100 ml. The distribution in the abundance of worms in this instance did not reflect the most polluted area of the lake as indicated by bacterial counts. The apparent reason for the abundance of worms in the middle and river side of the lake was that the soil of the lake bottom there contained less sand than did the lake bottom on the cottage side.

INSECTA: — All insects collected were in either the larval or pupal stage. Most of the insects taken were dipterous larvae except for the collections from Middle Quiver Lake where the weight of mayfly nymphs (*Hexagenia limbata*) comprised 75.4 percent of the insects taken. On the basis of numbers, mayfly nymphs formed only 11.8 per cent of the total number of insects from Middle Quiver Lake. In Lower Quiver Lake *Hexagenia limbata* comprised 43.0 per cent of the total weight of all insects. The numbers of mayfly nymphs collected in Middle Quiver Lake ranged from 0 in 1958 to 8 per square foot in 1954. In the collections from Lake Chautauqua and Lake Matanzas mayfly nymphs were either scarce or absent. Even though Lake Chautauqua and Quiver Lake were adjoining lakes and were connected during periods of high river stages, no specimen of *Hexagenia limbata* occurred in the collections from Lake Chautauqua.

Trichoptera larvae from Lake Chautauqua and Quiver Lake were confined to the one species, *Oecetis inconspicua*. In Lake Chautauqua the single species of Trichoptera comprised 0.3 per cent of the total number of insects taken in the benthic collections which on a weight basis amounted to 2.0 per cent of the total weight of insects. Trichop-

tera larvae formed less than 1.0 per cent of the total number and weight of insects taken from Middle Quiver Lake. No Trichoptera larva appeared in the collections from Lake Matanzas.

Odonata, Coleoptera and Megaloptera larvae were scarce in the benthic collections from all three lakes and formed only a small, minor part of the insect fauna. Damselfly nymphs, however, did occur abundantly on sago pondweed plants in Lake Chautauqua.

A summary is given in Table VI of the dipterous larvae collected in the bottom samples of these lakes. *Chaoborus* sp. was the most common dipterous larva taken at Lake Matanzas. This form was quite scarce in the collections from the other lakes. The scarcity of *Chaoborus* in Lake Chautauqua may have been related to the shallowness of that lake as compared with the greater depths present at Lake Matanzas (Tables II & IV). Cronk (1932) working in Ontario found that *Chaoborus* did not occur in depths of less than 20 feet, and that large lakes were not suitable for the genus.

Dipterous larvae of the genera *Pelopia, Procladius* and *Coelotany-*

TABLE VI.—Kinds, average numbers and wet weights of dipterous larvae per square foot at Lake Matanzas, Middle Quiver Lake and Lake Chautauqua, Illinois

Kinds	Lake Matanzas[1]		Quiver Lake[2]		Lake Chautauqua[1]	
	No.	Per-cent	No.	Per-cent	No.	Per-cent
Chaoborus sp.	38	27.5	*	–	*	–
Pentaneura sp.	0	–	1	3.6	1	0.3
Anatopynia sp.	0	–	0	–	*	–
Pelopia sp.	31	22.5	7	25.0	121	38.9
Procladius sp.	22	15.9	8	28.5	93	29.9
Coelotanypus sp.	17	12.3	8	28.5	40	12.9
Cricotopus sp.	0	–	0	–	*	–
Hydrobaenus sp.	0	–	*	–	0	–
Tendipedini (Tribe)	0	–	0	–	5	1.6
Polypedilum sp.	*	–	0	–	0	–
Cryptochironomus sp.	1	0.7	1	3.6	4	1.3
Tendipes spp.	3	2.2	1	3.6	23	7.4
Glyptotendipes sp.	0	–	0	–	*	–
Palpomyia sp.	22	16.0	1	3.6	21	6.7
Undetermined	4	2.9	1	3.6	3	1.0
Total	138	100.0	28	100.0	311	100.0
Weight in Grams	0.21	–	0.05	–	0.73	–

[1] 1952-56.
[2] 1952-58.
* Denotes less than 0.5 organism per square foot.

pus were common in the collections from all three lakes. At Lake Chautauqua *Tendipes* spp. varied from 1 to 61 organisms per square foot during the 1952-56 period and formed an important part of the dipterous weight from that lake.

We believe that the scarcity of dipterous larvae in Quiver Lake was related to the abundance of snails and other mollusca that occurred in that lake (Fig. 6). The effects snails have upon dipterous larvae and other organisms were discussed in some detail by Richard-

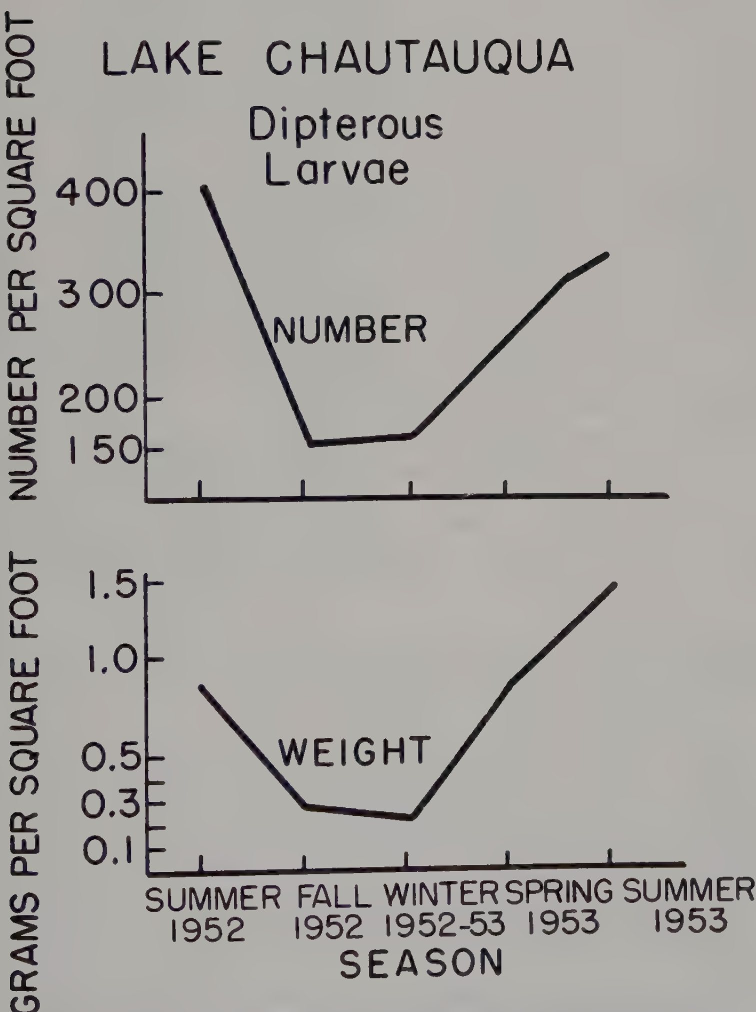

Fig. 8.—Seasonal fluctuations of standing crops of dipterous larvae at Lake Chautauqua, Illinois (1952-53).

son (1928). It will be noted in Figure 7 that some increase occurred in the dipterous larvae population in Quiver Lake following the decline that occurred in the mollusca population after 1952. Dipterous larvae populations in Lake Chautauqua and Lake Matanzas were evidently benefited by the scarcity of snails in those lakes.

Considerable seasonal variation was found to occur in the dipterous larvae population in Lake Chautauqua (Fig. 8), during the 1952-53 period. The summer collections in both 1952 and 1953 contained greater numbers and weights of dipterous larvae than did the collections made in the fall, winter, and spring. The scarcity of dipterous larvae in the fall and winter collections was quite contrary to findings made by other workers (Lundbeck, 1926; Eggleton, 1931; Lindeman, 1942; Ball and Hayne, 1952; Anderson and Hooper, 1956; and others). Lindeman, Ball and Hayne all mentioned, however, that a decline in numbers of dipterous larvae occurred under the ice cover during the winter months. The reduced numbers and weights of dipterous larvae in our fall collections may have been a result of the presence in the lake of small dipterous larvae capable of passing through the No. 30 sieve used in washing the samples. The winter collections may have been low due to the loss of larvae passing through the sieve, plus the fact that the collections were taken in January rather than prior to the time ice cover was formed. The data presented in Figure 8 for Lake Chautauqua indicated that large standing crops of dipterous larvae were present in the lake during the normal growing season of fishes.

On the basis of the seasonal variations of dipterous larvae determined for Lake Chautauqua, it appeared that the low standing crops of dipterous larvae at Lake Matanzas in 1952 and 1954 through 1956 may have been a result of our taking the samples in the fall rather than in the summer or spring. The highest standing crop of dipterous larvae recorded for Lake Matanzas was in 1953, the only year samples were taken in the spring and summer months from that lake (Fig. 7). Therefore, the standing crop of dipterous larvae data for Lake Matanzas, other than the year 1953, probably should not be used for comparitive purposes with the Lake Chautauqua and Quiver Lake data (Fig. 7 and Table V).

No attempt was made in this investigation to identify the dipterous pupae collected. At Lake Chautauqua dipterous pupae accounted for 0.6 per cent of the total number of insects collected and 2.0 per cent of their total weight. A total of four dipterous pupae altogether was taken in the Lake Matanzas and Middle Quiver Lake benthic collections.

MOLLUSCA: — All of the mollusca taken in the benthic samples at Lake Matanzas were fingernail clams. At Lake Chautauqua fingernail clams amounted to 97.0 per cent of the mollusca by numbers and 99.0 per cent by total weight. A few specimens of the snail *Valvata tricarinata* comprised the remainder of the mollusca collections from Lake Chautauqua.

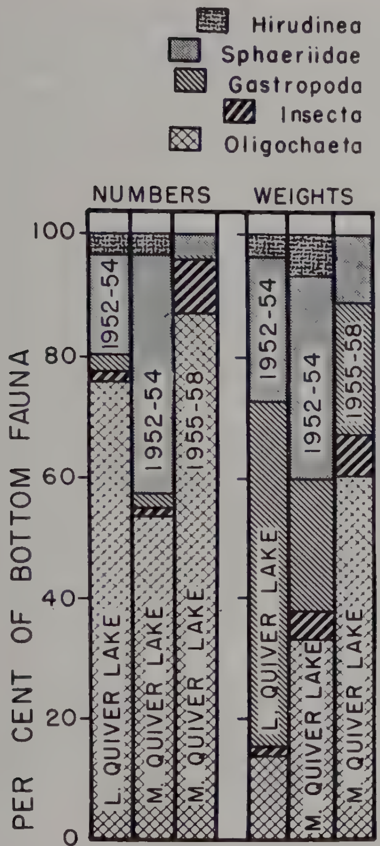

Fig. 9. — Composition of bottom fauna organisms at Lower Quiver Lake (1952-54) and Middle Quiver Lake (1952-54; 1955-58), Illinois.

Fingernail clams disappeared from the collections at Lake Matanzas after 1953, and after 1954 they became scarce at Lake Chautauqua (Fig. 7).

In 1952 fingernail clams were extremely abundant in Middle Quiver Lake, amounting to 2,286 per square foot with a weight of 6.71 grams (excluding shell weights). In the following year their numbers dropped to 103 per square foot with a weight of 0.48 grams. Between 1954 and 1958 the numbers of fingernail clams varied between 0 and 50 per square foot in Middle Quiver Lake. At Middle Quiver Lake in the 1952-54 period fingernail clams comprised 59.4 per cent of the total weight of mollusca (Fig. 9); whereas, in the 1955-58 period they amounted to only 29.5 per cent.

A similar decline also occurred in the fingernail clam population of Lower Quiver Lake. The fingernail clam population at that lake dropped from 1,115 per square foot in 1952 to 54 in 1953 and to 0

in 1954. At Lower Quiver Lake in the 1952-54 period (only data available) fingernail clams comprised only 29.2 per cent of the total weight of mollusca collected from that portion of the lake (Fig. 9).

Snails comprised the remainder of the above mentioned mollusca weights at Quiver Lake. A summary of the snail data from Quiver Lake is presented in Table VII. In 1952 snails were very abundant in both Lower and Middle Quiver Lake. At Lower Quiver Lake snails decreased from 10.76 grams (excluding shell weights) in 1952 to 6.07 grams in 1954. All of the species of snails there declined in abundance with the exception of *Pleurocera acuta*. During the 1952-54 period at Lower Quiver Lake the species *Campeloma decisum* comprised 45.6 per cent of the total snail weight. This species comprised only 11.7 per cent of the total snail weight in Middle Quiver Lake. The difference in abundance of *Campeloma decisum* between the two sections of the lake was thought to have been associated with water current. Baker (1928) reported that *Campeloma decisum* was found in the presence of a current. The lack of current in Middle Quiver Lake at times of low water levels probably pre-

TABLE VII.—Species composition, average numbers and wet weights of snails per square foot at Lower Quiver Lake (1952-54) and Middle Quiver Lake (1952-54 and 1955-58), Illinois

Species	1952-1954				1955-1958	
	Lower Quiver Lake		Middle Quiver Lake		Middle Quiver Lake	
	No.	Per-cent	No.	Per-cent	No.	Per-cent
Valvata tricarinata	*	–	1	1.7	0	–
V. lewisi	*	–	0	–	0	–
Viviparus contectoides	8	9.8	2	3.5	*	–
V. intertextus ill.	4	4.9	1	1.8	0	–
Lioplax subcarinata	*	–	*	–	0	–
Campeloma integrum	1	1.2	0	–	*	–
C. rufum	*	–	0	–	0	–
C. decisum	17	20.7	1	1.8	0	–
Amnicola limosa	2	2.4	1	1.8	0	–
Cincinnatia emarginata	31	37.8	48	84.2	0	–
Pleurocera acuta	19	23.2	3	5.2	1	100.0
Undetermined young	*	–	*	–	0	–
Total	82	100.0	57	100.0	1	100.0
Weight in grams (excluding shells)	11.45		1.68		0.48	

* Denotes less than 0.5 organisms per square foot.

vented the species from occurring as abundantly as it did in Lower Quiver Lake where a current was always present.

At Middle Quiver Lake in 1952 the snail population was 124 per square foot with a weight of 3.35 grams (excluding shell weight). The snail population dropped in 1953 to 44 per square foot (weight was 0.87 grams) and from 1954 through 1957 the population ranged from 1 to 2 snails per square foot (weight ranged from 0.39 to 1.01 grams). Table VII reveals the changes that occurred in the various species of snails at Middle Quiver Lake between the periods of 1952-54 and 1955-58. After 1952 the small snail *Cincinnatia emarginata* began to decline in numbers, and by 1954 the species was completely absent from the collections (Fig. 10). The species followed a similar decline in the collections from Lower and Upper Quiver Lake. Collections made in the years after 1953 failed to reveal the presence of *Cincinnatia emarginata* in any of the three sections of the lake sampled.

HIRUDINEA: — Leeches comprised only a small part of the bottom fauna collections from Lake Chautauqua and Lake Matanzas (Tables V and VIII and Fig. 6). In 1952 leeches were abundant in Middle Quiver Lake where the standing crop was 134 per square foot. Most of the leech population was comprised of *Helobdella stagnalis.* A drastic decline occurred in the leech population in Middle Quiver Lake after 1952 which paralleled the declines of *Cincinnatia emarginata* and fingernail clams (Fig. 10). No leech was taken in the Middle Quiver Lake collections after 1954. Richardson (1928) noted in his studies on the Illinois River that increases in fingernail clam populations possibly were checked by leech predation. In the present study (Fig. 10) it appeared that the decline and final dis-

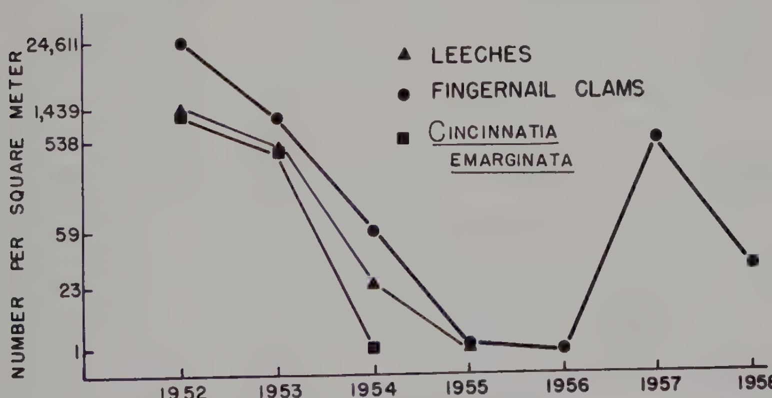

Fig. 10.—Predator-prey relationship is shown between leeches and small mollusca at Middle Quiver Lake, Illinois (1952-58). The number of organisms per square meter is plotted on semi-log paper. (Less than 1 organism per square meter is 0.)

appearance of leeches in Middle Quiver Lake was related to the collapse of the small mollusca populations which had probably served as prey for the leeches.

Bottom Fauna in Relation to Waterfowl

In late winter and early spring of 1953 lesser scaup ducks (*Athya affinis*) occurred abundantly on Quiver Lake. The maximum number of scaup ducks present at one time on the lake that year was about 20,000. Since 1953 very few scaup ducks have used the lake. The maximum number we have seen on the lake since 1953 has been less than 1,000 birds.

The lesser scaup ducks were observed on numerous occasions by us in early 1953 to be diving apparently for small mollusca which were then abundant in the lake. Bent (1951) and Cottam (1939) listed small mollusca as part of the diet of the lesser scaup duck. We believe that the scarcity of scaup ducks on Quiver Lake after early 1953 was associated with the disappearance of small snails and the decline of fingernail clams that occurred at that time (Fig. 10). The temporary slight increase that occurred in the fingernail clam population in 1957 (Fig. 10) did not result in an increased usage of the lake by scaup ducks.

Pollution Caused by Waterfowl

Lake Chautauqua is used by large concentrations of migrating waterfowl chiefly during the months of late October, November, and December. Mallards (*Anas platyrhynchos*) comprise the bulk of the waterfowl that use the lake. These migrating birds do most of their feeding in local fields on corn that is knocked to the ground by mechanical corn pickers (Bellrose, 1954).

The waterfowl census data given below were furnished to us by Mr. Frank C. Bellrose of the Illinois Natural History Survey. On September 10, 1953 there were 200 ducks on Lake Chautauqua, and by November 5th the number of ducks had increased to 62,000. During that period the coliform count in the middle of the lake ranged from <23 to 60 MPN/100 ml and the enterococcus count ranged from <6 to 23 MPN/100 ml. The waterfowl count on the lake from November 12 to December 7, 1953, varied from 195,000 to 205,000 ducks. The bacterial counts made from water samples collected on December 8, showed a definite increase over the earlier fall counts. The coliform count in December was 230 MPN/100 ml and the enterococcus count was 6,200 MPN/100 ml. We believe that the increase in the bacterial counts in December was associated with the rise in the duck population on the lake.

Detailed studies of pollution caused by domestic ducks have been reported by various persons working in New York State. Redfield (1952) estimated that 2.7 million pounds of nitrogen and 0.82 million pounds of phosphate are available annually from duck farms on tributaries of Moriches Bay and on the Carmans River, New

York, where 4 million domestic ducks are produced annually. From this same area Ryther (1954:207) found that: "Although the bays were heavily enriched only during the duck growing season, relatively high concentrations of nutrients appear to be present throughout the year, presumably from the decomposition of the rich sediments in the tributaries receiving the duck farm effluents." Stall and Melsted (1951:12) reported concerning the sediment characters of Lake Chautauqua, Illinois, that: "The total carbon and total nitrogen values are extremely high, indicating an accumulation of organic matter in the lake far in excess of any amounts that could be accounted for through soil erosion. These large accumulations of nitrogen and carbon must, therefore, be attributed to wildlife excreta." The water analyses for Lake Chautauqua did not reflect an increase in nutrient materials during the height of duck usage on the lake in the late fall of 1953.

In the fall, winter, and spring of 1954-55, 20,000,000 duck-days were spent on Lake Chautauqua. It was considered that these ducks spent a part of their time on other waters or in cornfields feeding. Mr. Bellrose believed that a conservative estimate of actual use of the lake by the ducks would have been 80 per cent of the total duck-day value or 16,000,000 continuous duck-days on the lake. In the studies made by the New York State Water Pollution Board in Suffolk County (Sanderson, 1953) it was found that the raw wastes produced daily by 1,000 domestic ducks contained an average of 5.7 pounds total nitrogen, 7.6 pounds of total phosphate, and 3.6 pounds of soluble phosphate. Since domestic ducks are fed large quantities of prepared feeds by man their wastes would be expected to be higher in nutrients than those of wild ducks. In order to apply the above domestic duck waste values to wild ducks at Lake Chautauqua we arbitrarily used 0.50 as a correction factor to compensate for differences in food intake and smaller size of the birds. The resulting estimate of fertilizer materials deposited by waterfowl in Lake Chautauqua on a per acre basis each year in the 1954-55 period was as follows: 12.8 pounds of nitrogen, 17.1 pounds of total phosphate, and 8.1 pounds of soluble phosphate.

Ducks were on Lake Matanzas and Quiver Lake for approximately 100,000 duck-days each year. In an earlier section of this paper it was shown that the dipterous larvae population was much higher in Lake Chautauqua than in the other two lakes studied. We believe that the nutrients added to Lake Chautauqua annually by waterfowl were largely responsible for the large standing crops of dipterous larvae. Jackson and Starrett (1959) considered the following factors also of importance in affecting the productivity of Lake Chautauqua: (1) lack of summer stagnation; (2) shallowness of the lake; and (3) addition of nutrients from the river.

SILTATION

Siltation that is occurring in the Illinois River flood plain lakes

is drastically reducing their storage capacities. In the three lakes studied silt has been deposited at a high annual rate since the early 1930's (Jackson and Starrett, 1959).

Ellis (1931) discussed the adverse effects of silt upon snails in the Mississippi River. We have theorized that the scarcity of snails in Lake Chautauqua and Lake Matanzas may have been caused by siltation. In those lakes current was seldom perceptible, whereas in Quiver Lake current was present except during low river stages. The absence of current in Lake Chautauqua and Lake Matanzas may permit suspended silt particles to settle over young snails and smother them. In Quiver Lake the current may have prevented the silt from settling at a rate sufficient to suffocate young snails. The results of the present study suggest that the scarcity of snails in Lake Chautauqua and Lake Matanzas may allow dipterous larvae to utilize the increased enrichment of bottom soils caused by human, duck and silt pollution.

In 1952 and 1953, the bottom fauna at Middle Quiver Lake was rich in mollusca and supported only a small dipterous larvae population, a situation similar to that found in the earlier years of "cleaner water" in the Lower Illinois River (Richardson, 1921a). In contrast, large dipterous larvae populations occurred in Lake Chautauqua and Lake Matanzas in 1953.

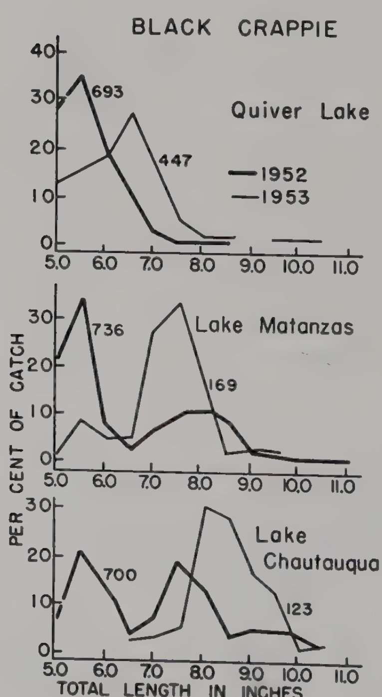

Fig. 11.—Length-frequency distribution of black crappies taken in 1-inch wing net collections during early fall months (1952 and 1953) at Quiver Lake, Lake Matanzas and Lake Chautauqua, Illinois. Number of fish measured accompany each graph.

An attempt was made to correlate growth of the black crappie with the abundance of dipterous larvae. Length-frequency data for black crappies collected in the fall months of 1952 and 1953 from Quiver Lake, Lake Matanzas and Lake Chautauqua are presented graphically in Figure 11. We were not able to age the black crappies from Quiver Lake with any degree of accuracy; however, rate of growth of black crappies collected from Lake Matanzas and Lake Chautauqua was considered good. The length-frequency graphs indicated that Lake Matanzas and Lake Chautauqua contained black crappies of sizes useful to anglers (8 inches), whereas, the black crappies in Quiver Lake were mostly of undesirable sizes. We believe the poor growth of black crappies in Quiver Lake was related, at least in part, to the scarcity of dipterous larvae in that lake. On the other hand, we hypothesize that the abundance of dipterous larvae in Lake Chautauqua and Lake Matanzas may have been an important factor to the rapid growth of black crappies in those lakes.

CHANGES IN BOTTOM FAUNA

The benthic studies made in Lower Quiver Lake in the 1952-54 period are of particular interest here since that section of the lake is actually a part of the Illinois River investigated by Richardson (1928) between 1913 and 1925 (Figs. 1 and 3). Richardson found in the cleaner water period of 1913-15 that snails formed an impor-

TABLE VIII.—Species composition and average numbers of leeches per square foot at Lake Matanzas, Middle Quiver Lake and Lake Chautauqua, Illinois

Species	Lake Matanzas[1] No.	Lake Matanzas[1] Per-cent	Quiver Lake[2] No.	Quiver Lake[2] Per-cent	Lake Chautauqua[1] No.	Lake Chautauqua[1] Per-cent
Helobdella stagnalis	*	–	21	84.0	1	33.3
H. elongata	1	100.0	3	12.0	2	66.7
H. lineata	0	–	*	–	0	–
Erpobdella punctata	*	–	1	4.0	0	–
Glossiphonia complanata	0	–	*	–	0	–
Placobdella montifera	*	–	*	–	0	–
Myzobdella moorei	0	–	*	–	*	–
Actinobdella inequiannulata	0	–	0	–	*	–
Dina sp.	0	–	*	–	0	–
Undetermined	0	–	*	–	0	–
Total	1	100.0	25	100.0	3	100.0

[1] 1952-56.

[2] 1952-58.

* Denotes less than 0.5 organism per square foot.

tant part of the bottom fauna in all reaches of the river between Chillicothe and Beardstown. The snails collected in the 1913-15 period included at least one-half dozen species sensitive to pollution. Some of those species were: *Viviparus contectoides, Lioplax subcarinata, Amnicola emarginata* (probably *Cincinnatia emarginata*) and *Amnicola limosa.* By 1920 these more sensitive species were practically wiped out by pollution from the deeper open water of the river between Chillicothe and Beardstown. Richardson (1928:430) stated that: "Below Peoria, in the 10 miles between Havana and Liverpool, where the combined *Gastropoda* had averaged 496 per square yard in 1915, they rose in 1925 to a bit less than 40, from just half that number at the recorded low point five years before. The fact that more than half of the specimens taken in this section in 1925 were *Vivipara contectoides,* however, (the rest being *Campeloma subsolidum*) seems to reflect to some extent the results of the previously mentioned improvement in the bottom dissolved oxygen supply below Copperas Creek Dam since 1923." Further improvement in the condition of the river has occurred since 1925 as was shown by our collections from Lower Quiver Lake in the 1952-54 period (Table VII) where water-breathing snails averaged 738 per square yard.

Richardson (1921a) took bottom samples at Lake Matanzas in the summer of 1915 and at Quiver Lake in 1914, 1915 and 1920. A comparison is made in Table IX of Richardson's bottom samples

TABLE IX.—Numbers of bottom fauna organisms per square yard at Lake Matanzas, Illinois, 1915 and 1953 (Summer)[1]

Organisms	Year 1915[2] Number	Year 1915[3] Number	Year 1953 Number
Campeloma subsolidum	0.0	5.0	0
Pleurocera sp.	0.0	1.6	0
Viviparus contectoides	0.0	8.3	0
Valvata spp.	14.4	3.3	0
Sphaeriidae	269.9	63.3	180
Sub-total	284.3	81.5	180
Dipterous larvae and pupae	23.3	2.3	2,790
Hexagenia, etc., nymphs	0.0	6.6	0
Caenis nymph	0.0	3.3	0
Leeches	30.7	13.8	63
Oligochaeta	4.4	0.0	11,007
Total	342.7	107.5	14,040

[1] 1915 data after Richardson (1921a:506-507).

[2] Depth, 6.5 to 8.5 feet, no vegetation.

[3] Depth, 2 to 6 feet, some vegetation at all stations.

from Lake Matanzas with our collections taken there in 1953. It is apparent from Table IX that some major changes have occurred in the bottom fauna at Lake Matanzas since 1915. In that year snails were common in the lake, whereas, in 1953 none were taken in our samples. Numbers of *Oligochaeta* and dipterous larvae have greatly increased in the lake since 1915. Richardson collected 6.6 *Hexagenia* sp. nymphs per square yard in one series of collections from Lake Matanzas in 1915, while through the entire 1952-56 period only 1 specimen of *Hexagenia* was taken from that lake. Possibly the reduction that occurred in mayfly nymphs in the lake was caused by competition with dipterous larvae, as the latter greatly increased in the lake sometime after 1915.

In Table X a comparison is made between Richardson's (1921a) 1914 and 1915 bottom samples from Quiver Lake and our 1952 and 1954 samples from Middle Quiver Lake. In 1914 and 1952 mollusca were abundant in Quiver Lake; however, species of small snails and

TABLE X.—Numbers of bottom fauna organisms per square yard at Middle Quiver Lake, Illinois, 1914-15 and 1952 and 1954[1]

Organisms	Year 1914 No.	1915 No.	1952 No.	1954 No.
Campeloma subsolidum	24.7	0.0	0	0
Lioplax subcarinata	11.1	0.0	3	0
Viviparus contectoides	48.2	7.1	45	9
Pleurocera sp.	1.1	0.0	45	9
Other species of large snails	0.0	0.0	63	3
Amnicola emarginata	42.3	0.0	0	0
Amnicola limosa	8.2	16.0	3	0
Valvata spp.	9.4	0.0	3	0
Physa, small	7.6	0.0	0	0
Other species of small snails[2]	0.0	0.0	963	0
Sphaeriidae	50.2	1.0	20,574	54
Sub-total	202.8	24.1	21,699	75
Dipterous larvae and pupae	38.9	176.3	135	411
Trichoptera larvae	0.5	0.0	9	0
Hexagenia nymph	0.5	0.0	27	72
Agrionid nymph	1.1	2.1	0	0
Libelluid nymph	1.6	0.0	0	0
Leeches	37.6	11.9	1,215	24
Oligochaeta	11.7	0.0	13,716	4,347
Coleoptera larvae	0.0	0.0	0	3
Total	294.7	214.4	36,801	4,932

[1] 1914-15 data after Richardson (1921:505-506).

[2] Refers to *Cincinnatia emarginata* which is probably the same species Richardson identified as *Amnicola emarginata.*

fingernail clams (chiefly young) were more abundant in the lake in 1952 than in 1914. The species *Cincinnatia emarginata* which occurred so abundantly in the 1952 collections (Fig. 10) was probably the same species that Richardson identified in his 1914 collections as *Amnicola emarginata. Campeloma subsolidum,* later referred to as *Campeloma crassulum* (Baker, 1928), occurred abundantly in Richardson's 1914 collections but was not taken in the present study. The large snail *Viviparus contectoides* was common in collections from Quiver Lake in 1914 and 1952. Dipterous larvae were not abundant in the lake either in 1914 or 1952. The striking difference in the bottom fauna at Quiver Lake between the years 1914 and 1952 was the abundance of worms in the 1952 collections (Table X). In 1920 Richardson (1921b) found that Quiver Lake had only 48 worms per square yard on mud bottom and that the lake did not show the great increase in worms he found elsewhere along the river, following the severe pollution conditions that existed there during World War I.

Richardson's 1915 samples at Quiver Lake showed a sharp decline in the small mollusca population from the previous year (Table X). Similarly the mollusca population was greatly reduced at Quiver Lake in the 1952-58 period (Fig. 7 and Table X). Richardson (1921a) concluded that the severe decline in small mollusca in the 1914-15 period was due to some unexplained mortality. It is doubtful if the decline of mollusca in the 1952-58 period in Quiver Lake was related to an increase in pollution accompanied by a reduction in dissolved oxygen, since the mayfly nymph *Hexagenia limbata* remained abundant in the lake (Table X). Richardson (1928) considered *Hexagenia bilineata* an important clean water species and found it to be common in the river near Havana in the 1913-15 period and earlier. In 1920 Richardson failed to take that species of mayfly from the river 4 miles below Havana. Hunt (1953) stated that nymphs of *Hexagenia limbata* were unable to withstand stagnation conditions where the dissolved oxygen content of the water dropped below 1 ppm. We are, therefore, of the opinion that possibly the declines in mollusca populations at Quiver Lake noted by Richardson in 1915 and presently by ourselves were natural declines following periods of overpopulation of mollusca rather than a result of an oxygen deficiency caused by some form of pollution. However, there is also the possibility that one or more of the new organic chemical exotics in the river, such as detergents, could have adversely affected the molluscan population in Quiver Lake in 1953.

The great increases in worms that have occurred at Lake Matanzas and Quiver Lake since 1915 evidently resulted from pollution and siltation.

SUMMARY

This investigation was conducted to show the effects that various types of pollutants have had upon the bottom fauna organisms in

three Illinois River flood plain lakes. The lakes studied were in the vicinity of Havana, Illinois. Between 1952 and 1958, 363 bottom samples were taken with a 6 x 6-inch Ekman dredge. Results of chemical analyses indicated that all three lakes were rich in nutrients.

The annual standing crop of benthic organisms varied considerably in the three lakes. The average standing crop per square foot was: 495 organisms and 0.90 grams in Lake Matanzas; 1,108 organisms and 4.44 grams in Middle Quiver Lake; and, 886 organisms and 1.50 grams in Lake Chautauqua.

Dipterous larvae were never abundant in the collections from Quiver Lake; however, they formed an important part of the benthic collections from Lake Chautauqua and Lake Matanzas. Fertilizing materials deposited by migratory waterfowl together with the scarcity of snails were considered as factors contributing to the development of large standing crops of dipterous larvae in Lake Chautauqua. Species of the genera *Pelopia, Procladius* and *Coelotanypus,* were common dipterous larvae in the collections from all three lakes. *Chaoborus* sp. was the most common dipterous larva taken at Lake Matanzas, whereas, this form was scarce in the collections from the other two lakes studied.

On the basis of numbers, Oligochaeta comprised over 60 per cent of the bottom fauna from all three lakes.

Hexagenia limbata nymphs represented 75.4 per cent of the weight of the immature insects taken in the collections from Middle Quiver Lake. This species did not occur in the collections from Lake Chautauqua, and only one specimen of *Hexagenia* sp. was collected at Lake Matanzas.

Fingernail clams and water-breathing snails flourished in Quiver Lake in 1952. After 1952 the molluscan population of that lake declined sharply. Mollusca formed only a minor part of the bot om fauna of Lake Chautauqua and Lake Matanzas.

Leeches were abundant in Quiver Lake in 1952; however, a drastic decline occurred after 1952 which tended to parallel the decline of the small mollusca population. No leech was taken from Middle Quiver Lake after 1954.

A reduction in numbers of lesser scaup ducks using Quiver Lake occurred following a decline in the population of small mollusca of that lake.

Findings in the present study reveal some drastic changes in the bottom fauna of Quiver Lake and Lake Matanzas since 1914 and 1915. The most drastic change since that time has been the great increase in Oligochaeta. At Lake Matanzas the Oligochaeta population jumped from 4.4 per square yard in 1915 to 11,007 in 1953. A similar change has occurred in Quiver Lake. At Lake Matanzas the mollusca population has become greatly reduced since 1915 and the dipterous larvae population has increased. Siltation and other forms of pollution were considered important factors in the drastic changes that have occurred in the bottom fauna of the lakes studied.

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Mammals of the Santa Catalina Mountains, Arizona

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This paper is a compilation of mammal records from the Santa Catalina Mountains, Pima and Pinal counties, Arizona, based on the author's field work in the area and that of earlier investigators. The Santa Catalina Mountains are about ten miles north of Tucson and are between 32° 15′ and 32° 35′ north latitude and 110° 30′ and 111° west longitude. The boundaries, as herein defined in reference to landmarks, are as follows: Reddington Pass in the southeast; Tanque Verde and Rillito creeks, including Fort Lowell, in the south; the Oracle and Florence highway in the west; and east along State Highway 77 to Oracle in the north.

Among mammal collections from this area, those by the following individuals and institutions may be mentioned: (1) E. W. Nelson and other Biological Survey personnel (specimens reported in various issues of the *North American Fauna*), (2) W. W. Price (in Allen, 1895), (3) Edgar A. Mearns and Frank X. Holzner on the Mexican Boundary Survey (in Mearns, 1907), (4) J. Kenneth Doutt for Carnegie Museum (Doutt, 1934), (5) Lee R. Dice and Philip M. Blossom for the University of Michigan (in Dice and Blossom, 1937), (6) Kansas University in 1952, and (7) the University of Arizona.

Collecting and field work has been concentrated in the following localities: (1) Camp or Fort Lowell, about 2000 feet, an abandoned military post on the south bank of Rillito Creek, about six miles from the base of the mountains; cottonwoods and willows along the creek, desert shrubs on the adjoining outwash plain (bahada); (2) Molino Basin, 4000 to 4200 feet, south face; desert grassland; (3) Oracle, 4500 feet, a town in Pinal County; desert bahadas and slopes, desert grassland; (4) Peppersauce Canyon, about 4600 feet, north face, some eight miles southeast of Oracle; riparian vegetation, mainly sycamores, along Peppersauce Creek, evergreen woodland (encinal) on the hillsides; (5) mouth of Pima Canyon, about 3200 feet, south face; desert bahadas and rocky slopes; (6) Reddington Pass, 4000 to 4300 feet, the pass between the Santa Catalina Mountains and the Rincon Mountains in the southeast; rocky slopes; (7) Lower and Upper Sabino Canyons, 3000 to 3400 feet, south face; bahadas and rocky slopes; (8) Soldier Camp area, 7700 to 8000 feet, south face; pines and firs; (9) mouth of Soldier Canyon, 3000 feet, south face; bahadas and slopes; (10) near Stratton Mine, 4600 feet, north face; encinal; (11) Summerhaven area, 7600 to 8000 feet, south face; pines and firs.

The following abbreviations are used with the records of occurrence for each species (the number with each abbreviation in the following list refers to the number of specimens from the Santa Catalina Mountains herein reported from

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that collection): AMNH—American Museum of Natural History, New York (14); BS—United States Fish and Wildlife Service, Biological Survey Collections, Washington, D. C. (212); Carnegie—Carnegie Museum, Pittsburgh, Pennsylvania (61); CNHM—Chicago Natural History Museum (2); DRD—Donald R. Dickey private collection (4); KU—Museum of Natural History, University of Kansas, Lawrence (41); LACM—Los Angeles County Museum (3); MVZ—Museum of Vertebrate Zoology, University of California (36); SDSNH—San Diego Society of Natural History (7); Stanford—Department of Biology, Stanford University, Palo Alto, California (1); UA—Department of Zoology, University of Arizona, Tucson (330); UM—Department of Zoology, University of Michigan, Ann Arbor (probably around 250); and USNM—United States National Museum, Washington, D. C. (140).

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PHYSIOGRAPHY AND VEGETATION

Tucson is situated at an elevation of about 2400 feet, whereas the basal elevation of the Santa Catalina Mountains is 3000 to 3500 feet. This rise is caused by the ascent in the bahadas, or outwash plains, which form the floor of the Santa Cruz Valley. Mt. Lemmon, 9163 feet, is the highest point of the Santa Catalinas and is located near the west end of the main ridge. Reddington Pass, at 4300 feet, connects the Catalinas in the southeast with the Rincon Mountains. The Canada Del Oro and the San Pedro River receive the north face drainage, and Rillito Creek receives the south face drainage. The Rillito drains into the Santa Cruz River; both the Santa Cruz and San Pedro are tributaries of the Gila River, but seldom have sufficient flow to reach it. Topography is steep and rugged; the major streams possess steep gradients. There are no mountain meadows or parks in the Catalinas.

Doutt (1934:243-44) pointed out that the Catalinas belong physiographically to the Mexican Highland Section, but, since they are separated from the other local ranges by the San Pedro and Gila

Rivers, they are more closely related to the Mexican Cordillera than to the Rocky Mountains. This land relationship extends also to the flora and fauna.

The vegetation of the Catalinas consists of (1) desert, (2) encinal, and (3) forest (after Shreve, 1915). Characteristic plants of the desert bahadas are creosote-bush (*Larrea tridentata*), various prickly pears (*Opuntia*), paloverdes (*Cercidium*), mesquites (*Prosopis*), and species of *Acacia*. On the desert slopes above the bahadas the following plants become abundant: ocotillo (*Fouquiera splendens*), *Agave palmeri, Agave schotti, Yucca macracarpa,* desert-spoon (*Dasyliron wheeleri*), bear-grass (*Nolina*), manzanita (*Arctostaphylos*), and California rosewood (*Vanquelina californica*). Saguaros are generally distributed on the bahadas and slopes. The ground cover of the desert slopes is more extensive than in the bahadas due to the replacement of many desert species by grasses and shrubs.

On the south face of the mountains, at about 4000 feet, desert begins to marge into encinal (evergreen woodland). This transition requires only a few hundred feet of elevation, and is in reality a compressed desert grassland (C. H. Lowe, Jr., personal communication). It can be observed at such areas as Molino Basin. Mesquite or desert grassland is well developed on the north and east faces of the mountains at about the same elevation, mainly because of more gentle slope. Encinal in the Catalinas is an admixture of evergreen oaks (*Quercus oblongifolia, Q. arizonica, Q. emoryi*), junipers, and pinyon pines. It begins at about 4500 feet and grades into ponderosa pine (*Pinus ponderosa*) forest at about 6500 feet. The elevational limits of encinal depend on such factors as slope exposure and topographical irregularities (Shreve, 1922). A pine-oak woodland between oaks and ponderosa pine may be recognized.

Ponderosa pine is the dominant tree on south slopes from some 6000 feet to the summit of Mt. Lemmon. The subdominants of the ponderosa pine forest are ceanothus (*Ceanothus fendleri*), chokecherry (*Prunus virens*), silver-leaved oak (*Q. hypoleucoides*), and a deciduous species of oak (*Q. gambeli*) (Lowe, personal communication). Clumps of muhly (*Muhlenbergia longiligula, M. montana*) also are characteristic.

Firs (*Pseudotsuga taxifolia, Abies concolor, A. lasiocarpa arizonica*) occur in mixed stands with southwestern white pine (*P. strobiformis*) and ponderosa pine on north slopes up to about 7500 feet, at which elevation ponderosa pine begins to drop out. Quaking aspen (*Populus tremuloides*) is associated with the fir forest. Coniferous forest in the Catalinas thus consists of two segments, ponderosa pine forest and fir forest. There is no timberline.

Riparian habitats are also present. They may be recognized at the lower elevations by such deciduous trees as cottonwood (*Populus fremonti*), willows (*Salix*), sycamore (*Platanus wrightii*), walnut (*Juglans major*), and ashes (*Fraxinus*). In the oak and coniferous growth at the higher elevations, these are replaced by maples (*Acer*

glabrum, A. grandidentatum, A. negundo) and alders (*Alnus*).

See Lange (1959) for photographs of the study area. Figure 5 in that paper is a view in the northern foothills of the Catalinas, Figure 6 is a view of creosote-bush flats, and Figure 7 shows the vegetation at 6000 feet elevation in the Bear Canyon area, south face.

ACCOUNTS OF SPECIES AND RECORDS OF OCCURRENCE

The records for each species and subspecies are arranged by elevation, insofar as possible. The following is a list of specimens and records known to the author.

1. *Didelphis marsupialis virginiana* Kerr.—The opossum was apparently introduced into the study area in the late 1940's (Hock, 1952).

2. *Sorex vagrans monticola* Merriam.—Total, 6: Summerhaven, 7500 ft., 4 (3, BS; 1, SDSNH); Soldier Camp, 1 (Carnegie); Carter Canyon, 1 (UA).

3. *Notiosorex crawfordi crawfordi* (Coues).—The first specimen of the gray shrew from the Santa Catalina Mountains was collected by J. A. Munro among boulders in ponderosa pine and oak growth on February 10, 1951. Measurements, in millimeters, are: testes, 0; total length, 80; tail, 27; and hind foot, 10. One skull and a left mandible were recovered by the author from some 50 barn owl pellets collected on June 6, 1957, about five miles southwest of Oracle. The collecting locality was a 35 foot shaft along the Burney Mines road, with grasses, jumping cholla, prickly pear, paloverde, mesquites, acacias, and an occasional juniper constituting the major vegetation.

Total, 2: Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft., 1 (UA): Bear Canyon, 6000 ft., 1 (J. A. Munro).

4. *Macrotus californicus* Baird.—Total, 4: 9 m. N Tucson [ca. 3000 ft.], 1 (UM); Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft., 2 (UA); Virginia Mine, 5000 ft., 1 (UA).

5. *Choeronycteris mexicana* Tschudi.—Total, 5: Tunnels at narrows of Sabino Canyon, 1 (UA); Sabino Canyon, 1 (UA); Alamo Canyon tunnel, 10 mi. N Tucson, 3 (UA).

6. *Myotis yumanensis yumanensis* (H. Allen).—Total, 3: 2 m. N, 7 m. E Tucson, 1 (UA); Castle Rock Ranch, 3 m. N, 16 m. E Tucson, 1 (UA); Lower Sabino Canyon, 3000 ft., 1 (UA).

7. *Myotis velifer* ssp.—The first specimen of the cave myotis from the Catalinas was shot on June 12, 1957, as it was flying along a dry wash on the north face of the mountains.

Total, 1: Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft. (UA).

8. *Myotis thysanodes thysanodes* Miller.— The fringed myotis is herein reported for the first time. A female was collected on June 12,

1957, in a south-facing tunnel about one-hundred yards east of the *M. velifer* locality listed above.

Total, 1: Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft. (UA).

9. *Myotis volans interior* Miller.—Total, 5: Summerhaven (UM).

10. *Myotis californicus* ssp.—Total, 8: Santa Catalina Mts., 1 (BS); Lower Sabino Canyon, 3000 ft., 1 (UA); Oracle, Pinal Co., 5 (USNM); Summerhaven, 1 (UM).

11. *Myotis subulatus melanorhinus* (Merriam).—Total, 3: Santa Catalina Mts., 1 (AMNH); 2 m. N, 7 m. E Tucson, 1 (UA); Castle Rock Ranch, 3 m. N, 16 m. E Tucson, 1 (UA).

12. *Pipistrellus hesperus* ssp.—The pipistrel is an early-flying, common bat in the study area. Nine were seen in Upper Sabino Canyon between 6:15 and 6:27 PM on September 29, 1956 (sun set at 6:16). About 90 were seen on October 12, 1956, flying down the canyon. This flight lasted from 5:40 to 6:10 PM. Pipistrels were first seen on October 19 and 26, 1956, at 5:45 PM, five minutes before sunset. The Molino Basin specimen was shot in daytime flight in December, 1952.

Total, 6: 2 m. N, 7 m. E Tucson, 1 (UA); Sabino Canyon, 7 m. N, 2 m. E Tucson, 2 (UA); Lower Sabino Canyon, 3000 ft., 1 (UA); Molino Basin, 4300 ft., 1 (KU); 8 m. SE Oracle, 1 (UM).

13. *Eptesicus fuscus pallidus* Young.—W. W. Price, *in* J. A. Allen (1895: 247), stated that the brown bat was, "Abundant everywhere, from the desert region about Fort Lowell, to the summit of the Chiricahua Mountains [Cochise County], 10,000 feet above sea level."

Total, 15: Ft. Lowell [ca. 2000 ft.], 3 (LACM); 2 m. N, 7 m. E Tuscon, 3 (UA); Sabino Canyon, 7 m. N, 13 m. E Tucson, 1 (UA); Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft., 1 (UA); 8 m. SE Oracle, 2 (UM); Summerhaven, 1 (UM); Camp Lawton, Mt. Lemmon, 8000 ft., 1 (UA); Santa Catalina Mts., 3 (BS).

14. *Lasiurus borealis teliotus* (H. Allen).—Total, 2: Peppersauce Canyon, 8 m. SE Oracle (UM).

15. *Lasiurus cinereus cinereus* (Palisot de Beauvois).—Total, 2: Binghampton ponds, ca. 5 m. NE Tucson, 1 (UA); Tanque Verde Creek, E Tucson, 1 (BS).

16. *Corynorhinus townsendii pallescens* (Miller).—Total, 10: Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft., 6 (UA); tunnel at 4500 ft., 1 (UA); 5-½ m. S, 3 m. W Oracle, 4800 ft., 1 (UA); summit, Mt. Lemmon, 2 (KU).

17. *Antrozous pallidus pallidus* (Le Conte).—Total, 7: 2 m. N, 7 m. E Tucson, 4 (UA); Oracle, 3 (BS).

18. *Tadarida brasiliensis mexicana* (Saussure).—W. W. Price, *in* Allen (1895:246), remarked that this species was, ". . . exceedingly abundant at Fort Lowell through the month of May. Many specimens were taken in the cornice of the deserted hospital building."

Total, 3: 2 m. N, 7 m. E Tucson, 1 (UA); Lower Sabino Canyon, 1 (UA); Virginia Mine, 5000 ft., 1 (UA).

19. *Tadarida femorosacca* (Merriam).—Total, 6: 2 m. N, 7 m. E Tucson (UA).

20. *Eumops perotis californicus* (Merriam).—Total, 2: 2 m. N, 7 m. E Tucson (UA).

Of the 17 species of bats recorded above, *Myotis velifer* and *Myotis thysanodes* are listed for the first time. Reference to Table I will show that no bats have been collected in the area during January and February, and only six in the last two months of the year. This reflects on several factors: (1) concentration of collecting in the spring, summer, and fall months; (2) migration of some species; and (3) the apparent absence of hibernacula in the Santa Catalina Mountains.

TABLE I.—The 17 species of bats reported from the Santa Catalina Mountains, showing the sex, month of collection, and approximate elevation in hundreds of feet

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Macrotus			♂ 50	♀ 30							♂ ♀ 42		4
Choeronycteris						2♂ 2♀ 35			♀ 30				5
Myotis yumanensis				♀ 25		♀ 25			♀ 30				3
M. velifer													
M. thysanodes						♀ 42							1
M. volans						♂ 4♀ 75							5
M. californicus						♂ 75					♂ 30		2
				♀		♀							

TABLE I.—(*continued*)

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
M. subulatus				25		25							2
Pipistrellus				♀ 25		♂ ♀ 30	♂ 45			♂ 30		♂ 43	6
Eptesicus				♂ 3♀ 25- 30	♂ 42	6♂ 2♀ 20- 80	2♀ 45						15
Lasiurus borealis							♂ ♀ 45						2
L. cinereus				♂ 25	♀ 25								2
Corynorhinus			♂ 2♀ 42			♂ 42	♂ 48	♂ 45		2♂ 80- 90		2♂ 42	10
Antrozous			♂ 25	2♂ ♀ 25				3♀ 45					7
Tadarida brasiliensis			♂50 ♀25							♀ 30			3
T. femorosacca				4♂ 2♀ 25									6
Eumops				2♂ 25									2
Total ♂	–	–	4	10	1	12	3	1	–	4	2	3	40
Total ♀	–	–	3	10	1	12	3	3	1	1	1	–	35

21. *Lepus alleni alleni* Mearns.—W. W. Price found the Allen jackrabbit ". . . . abundant about Tucson and in lower portions of the desert belt." He found it ". . . on the gravelly hills bordering the Rillito at Fort Lowell, and on the immense mesquite and *Larrea* plains of Tucson." (*in* Allen, 1895: 201-202). Doutt (1934: 267) found *L. alleni* and *Lepus californicus eremicus* equally abundant in the desert regions. Vorhies and Taylor (1933: 480) state that *L. alleni* seems ". . . to prefer grassy slopes at moderate elevations. The animals seem to like the bahadas or mesas above the giant cactus belt [saguaro cactus], where grasses, mesquites, and catclaws abound. They occur

also, somewhat scattered, on the creosote desert, and even, at times, in the heavy mesquite growth along the valley bottoms. . . . *Lepus alleni* is rarely observed in broken or hilly country." Dice saw three in mesquite grassland six miles southeast of Oracle (Dice and Blossom, 1937: 40). The author has seen Allen jackrabbits at an elevation of 4000 feet in Reddington Pass. The vegetation in this locality consists of scattered oaks and junipers, a few mesquites, clumps of manzanita and bear-grass (*Nolina*), small cacti, and sparse grass. Two *alleni* have been seen in this hilly, rocky country. A critical density of encinal may determine the upper elevational limit of *L. alleni alleni*.

Total, 28: Ft. Lowell, 19 (13, AMNH; 6, BS); Tanque Verde, 1 (KU); Rillito Creek, 5 m. N Tucson, 3 (BS); mouth Bear Canyon, 1 (UM); mouth Soldier Canyon, 1 (Carnegie); Oracle, 3 (2, Carnegie; 1, BS).

22. *Lepus californicus eremicus* J. A. Allen.—W. W. Price (*in* Allen, 1895: 202) thought that this species was, "The common Jack Rabbit over the entire region to about 7000 feet elevation. In the desert region about Tucson, this species is somewhat supplanted by *Lepus alleni*." Vorhies and Taylor (1933: 480) regarded the distributional relationships of these two species to be as follows: "On the grassy bahadas at altitudes of perhaps 3,500 feet, the antelope jack rabbits [*Lepus alleni*] are usually several times as numerous as the *Lepus californicus* type; but in the mesquites along the valley bottoms, and on the barren creosote bush desert, the *L. californicus* type is usually more numerous." *L. c. eremicus* was reported by Dice and Blossom (1937: 40) to range from the desert to the lower oaks. Doutt (1934: 268) found *L. c. eremicus* common in the Catalinas to elevations of 4500 feet. He noted it as less common above 4500 feet and did not find any in the pines and firs.

The race, *eremicus*, seems to be unable to tolerate higher elevations, whereas *L. c. deserticola* and *L. c. texianus* in northern Arizona range to 7500 feet. The upper elevational limits for *L. c. eremicus* and *L. alleni alleni* appear to be about the same in the Catalinas, that is 4,500 to 4,700 feet.

Total, 22: Ft. Lowell, 8 (5, USNM; 3, BS); Tanque Verde, 1 (KU); Rillito Creek, 1 (BS); near Walnut, NW base Catalina Mts., 1 (Carnegie); Soldier Canyon, 5 (Carnegie); Oracle, 4 (2, BS; 2, Carnegie); 2 m. S, 2 m. E Oracle, 4500 ft., 1 (UA).

23. *Sylvilagus audubonii arizonae* (J. A. Allen).—The desert cottontail is an abundant animal in the desert regions, apparently reaching its upper elevational limit in the oaks. Sowls (1957: 234-35) discusses the distribution of the desert cottontail and reports that it is found in oak woodland in certain parts of southeastern Arizona. The two University of Arizona specimens come from the lower oaks.

Total, 23: Ft. Lowell, 13 (10, USNM; 3, BS); Tanque Verde, 1 (KU); Oracle, 7 (6, BS; 1, Carnegie); 1½ mi. S Oracle, 4500 ft., 1 (UA); 1½ m. S, 1½ m. W Oracle, 1 (UA).

24. *Citellus spilosoma canescens* (Merriam).—Merriam (1890:

38) designated Oracle in Pinal County as the type locality of *Spermophilus spilosoma macrospilotus,* now regarded as a junior synonym of *C. s. canescens.* The series at his disposal consisted of five topotypes and the holotype. These were again reported in *North American Fauna* number 56, page 126. These are the only spotted ground squirrels known from the study area.

Total, 6: Oracle, Pinal Co., (BS).

25. *Citellus variegatus grammurus* (Say).—Price (*in* Allen, 1895: 237-38) reported the rock squirrel to be common along brush fences at Fort Lowell in the summer of 1892, but found none in January 1894. Mearns (1907) found it from the low desert to the high mountains and thought it hibernated in winter at the high elevations. Doutt (1934: 254) recorded it in rocky situations from 2400 to 9400 feet. Dice and Blossom (1937: 21) found them in rocky areas in the Catalinas. They are common in rocky areas at the lower elevations of Sabino Canyon. The author has seen rock squirrels eating mesquite buds and climbing cottonwoods in desert shrub habitat on the San Xavier Mission, Pima County. There are no rock outcrops in this area.

Total, 31: Santa Catalina Mts., 3 (2, BS; 1, MVZ); Ft. Lowell, 2 (1, BS; 1, USNM); mouth of Soldier Canyon, 1 (Carnegie); Upper Sabino Canyon, 3100 ft., 1 (UA); Pima Canyon, 3500 ft., 1 (BS); Linda Vista Ranch, 2½ m. S Oracle, 1 (UA); 2 m. W Oracle, 1 (UA); Oracle, 5000 ft., 15 (BS); near Soldier Camp, 2 (Carnegie); Summerhaven, 4 (3, UM; 1, SDSNH).

26. *Citellus tereticaudus neglectus* (Merriam).—Price (*op. cit.*) and Mearns (1907) remarked on the abundance of the round-tailed ground squirrel. Dice and Blossom (1937: 21) noted their wide distribution on the sandy desert soils. None have been taken on the north face. *C. variegatus, A. harrisii,* and *C. tereticaudus* are conspicuous diurnal mammals in the lower elevations.

Total, 51: Ft. Lowell, 29 (16, BS; 13, USNM); Santa Catalina Mts., 2 (CNHM); Rillito Creek, near Ft. Lowell, 5 m. N Tucson, 2 (1 BS; 1, UM); 5 m. N Tucson, 1 (UM); Tanque Verde, 3 (KU); mouth of Sabino Canyon, 3 (KU); mouth of Soldier Canyon, 7 (Carnegie); Soldier Canyon, 4 (UM).

27. *Ammospermophilus harrisii harrisii* (Audubon and Bachman).—Price (*in* Allen, 1895: 241) and Mearns (1907) found the Harris ground squirrel a common inhabitant of the lower deserts. Mearns (1907) regarded it as abundant in the valleys, canyons, and river bottoms, and did not find it above 5200 feet elevation in the Santa Cruz Valley. Dice and Blossom (1937: 22) found them in many habitats, but with a spotty distribution.

Total, 68: Ft. Lowell, 5 (USNM); Catalina Mt. foothills, S face, 2400-3000 ft., 29 (13, UM; 7, USNM; 4, UA; 3, Carnegie; 2, BS); Catalina Mt. foothills, N face, 4200-4500 ft., 16 (15, UA; 1, UM); Oracle, 5000 ft., 18 (15, BS; 3, MVZ).

28. *Eutamius dorsalis dorsalis* (Baird).—Price (*op. cit.*) shot a

Gila or cliff chipmunk at 8000 feet elevation near snow in January. The preferred habitat seems to be wooded areas, but several have been taken below the oaks.

Total, 55: Pima Canyon, 3500 ft., 2 (BS); 9½ m. N, 3 m. E Tucson Court House, 4000 ft., 1 (UA); Oracle, 2 (BS); 8 m. SE Oracle, 3 (UM); 10 m. N, 17 m. E Pima Co. Courthouse, Tucson, 1 (UA); Santa Catalina Mts., 5100 ft., 1 (UA); near Soldier Camp, 7 (5, Carnegie; 2, MVZ); Summerhaven, 19 (BS, UM, UA, SDSNH); Santa Catalina Mts., 3 (USNM); Mt. Lemmon, 8800 ft., 2 (UA).

29. *Sciurus aberti aberti* Woodhouse.—The Arizona Game and Fish Commission released 31 males and 27 females in the Catalina Mountains in 1940 and 1941. The preferred habitat of the Abert squirrel is the ponderosa pine forest; sight records place their upper and lower limits in the firs and pinyon-juniper, respectively. Hunt data from the Arizona Game and Fish Commission for the Catalina Mountains reveals that 49 hunters bagged 105 Abert squirrels in 1953 and 23 hunters bagged 45 squirrels in 1955. (Information supporting recommendations to the Commission on 1956 hunting seasons).

Total, 7: 30 m. E Tucson on Mt. Lemmon Rd., 1 (UA); Mt. Lemmon Rd., 3 (UA); Rose Canyon, 5 m. above dam site, 1 (UA); Mt. Lemmon area, 7000 ft., 1 (UA); Marshall Saddle, 1 (UA).

30. *Sciurus arizonensis catalinae* Doutt.—Doutt (1931: 271) described *S. a. catalinae* from the Santa Catalina and Santa Rita mountains. The series consisted of one adult male and four adult females taken near Soldier Camp between August 17 and 30, 1927. These squirrels were feeding on white pine cones. Mearns (1907) reported them to feed on pine cone seeds, walnuts, acorns, berries, and green vegetation in the deciduous trees of canyons and streams at lower elevations. Price thought that they were ". . . probably found all through the lower pine zone, usually not overlapping the range of *S. aberti*." (*in* Allen, 1895: 245). Dice and Blossom (1937: 24) noted a few Arizona gray squirrels in the higher elevations. The rapid spread of the Abert squirrel in the Catalinas since its 1940 introduction may have acted adversely on an already small population of Arizona grays. The author knows of no reliable records of *S. a. catalinae* in the Catalinas in recent years.

Total, 14: Summerhaven, 6 (2, UM; 2, SDSNH; 1, UA; 1, BS); east side Santa Catalina Mts., 1 (USNM); near Soldier Camp, 8000 ft., 5 (Carnegie); Carter Canyon, 8000 ft., 1 (SDSNH); Mt. Bigelow, 8000 ft., 1 (MVZ).

31. *Thomomys bottae modicus* Goldman.—In a discussion of *Thomomys* in southeastern Arizona, Lange (1958) noted that: ". . . *Thomomys bottae* shows considerable variation that appears to be correlated with elevation. In general, gophers from the desert valley floors, such as those occurring in the lowlands along the Santa Cruz and San Pedro Rivers, are large and light-colored. Gophers from the pine forests on the mountain tops, such as those from the Santa Catalina and Rincon Mountains, are smaller and dark-colored.

Specimens from the pine belt of the Santa Catalina Mountains are . . . referred to *Thomomys bottae catalinae.* Specimens from the Santa Cruz River Valley are referred to *T. b. modicus.* The pocket gophers from Molino Basin . . . and from Reddington Pass . . . exhibit a combination of characters that appears to be a more or less random mixture of features of the adjacent lowland form, *T. b. modicus,* and adjacent pine zone forms, *T. b. catalinae* and *T. b. hueyi.* Although this morphological intermediate form has been named (as *T. b. parvulus* by Goldman, 1947: 26) additional specimens not available to the original describer have demonstrated that the supposed diagnostic characteristics do not exist. The small size supposed to be diagnostic of these gophers was evident in the specimens available to Goldman but further collecting at the type locality (Reddington Pass) revealed that all specimens available to Goldman were either juveniles, subadults, or young adults." These intergrades are referred to *T. b. modicus.*

Total, 34: Univ. Ariz. Agric. Exp. Farm, 5 (UA); Tucson, 2 (UA); 3 m. N Tucson, Oracle Rd., 2 (UA); 5 m. NW Univ. Ariz. Agric. Exp. Farm, 1 (UA); 5 m. N Santa Cruz R. bottoms, 1 (UA); Canada del Oro, 16 m. N Tucson, 3 (UA); Sabino Canyon, 12 m. NE Tucson, 3000 ft., 4 (UA); 10 m. N, 17 m. E Pima Co. Courthouse, 1 (UA); Santa Catalina Mts., S slope, Molino Basin, 4200 ft., 10 (intergrades) (KU); Reddington Pass, 12 m. E Tanque Verde Rd., 5 (intergrades) (UA).

32. *Thomomys bottae catalinae* Goldman.—Total, 12: Summerhaven and Mt. Lemmon area (UA).

33. *Perognathus flavus flavus* Baird.—The silky pocket mouse is known only from Ft. Lowell. "Mr. Miller found it not uncommon in the sandy fields around Fort Lowell." (Price, *in* Allen, 1895: 215). Dice and Blossom (1937: 26) trapped one in 1930 among cottonwoods and willows and regarded it as probably rare in the Tucson area. Total, 7: Ft. Lowell (4, USNM; 2, BS; 1, UM).

34. *Perognathus amplus taylori* Goldman.—L. H. Miller took one in sandy soil at Fort Lowell in 1894 (Allen, 1895). Dice and Blossom (1937: 26) found the Arizona pocket mouse most common on the sandy desert soils; none were collected above 4000 feet elevation. They trapped three animals eight miles north of Tucson in sand and small gravel and in palo-verde and brittle-bush, and trapped two others nine miles north of Tucson on gravelly and rocky slopes.

Total, 9: Ft. Lowell, 1 (USNM); 8 m. NE Tucson, near Ft. Lowell, 3 (UM); 8 m. N Tucson, 2700 ft., 3 (UM); 9 m. N Tucson, 2 (UM).

35. *Perognathus penicillatus pricei* J. A. Allen.—Dice and Blossom (1936: 27) found the desert pocket mouse in sandy and gravelly soils.

Total, 62: Ft. Lowell, 39 (BS); near Ft. Lowell, 13 (UM); 8 m. N Tucson, 6 (UM); 9 m. N Tucson, 2 (UM); 10 m. N Tucson, 2 (UM).

36. *Perognathus intermedius intermedius* Merriam.—Price re-

ported: "This is the common Pocket-mouse of the region south of the Mogollon Mesa, where it outnumbers all the others, three to one. We found it especially abundant at Fort Lowell . . . but as none were obtained at Fort Lowell in January, it is not unlikely that it hibernates during the colder months." (*in* Allen, 1895: 218-19). Dice and Blossom (1937: 28) also attest to its abundance: ". . . probably the most abundant mammal in the deserts of southern Arizona and northern Sonora." It has been taken on the north face in rocky habitat: three miles southeast of Oracle in open encinal, and in Peppersauce Canyon among ocotillo (Dice and Blossom, 1937: 29).

Total, 78: Ft. Lowell, 46 (USNM); 8 m. N Tucson, 1 (UM); 9 m. N Tucson, mouth Pima Canyon, 18 (UM); 10 m. N Tucson, 9 (UM); 3 m. SE Oracle, 4500 ft., 1 (UM); 8 m. SE Oracle, 4700 ft., 3 (UM).

37. *Perognathus baileyi baileyi* Merriam.—Dice and Blossom (1937: 26) recorded the Bailey pocket mouse as numerous on the rocky bahadas, but rare on the sandy desert soils. It has been taken in grassland on the north face at 4700 feet elevation.

Total, 57: near Ft. Lowell, 6 (UM); Santa Catalina Mt. foothills, S face, 32 (25, UM; 5, UA; 1, BS; 1, Carnegie); Oracle, 1 (BS); 2½-10 m. SE Oracle, 4400-4700 ft., 18 (13, UM; 5, UA).

38. *Dipodomys spectabilis* ssp.—Bannertail kangaroo rats are not common in the study area. Their mounds seem to be most numerous in the foothill country west and north of the mountains. Gibbs (1955) trapped an immature male among a group of mounds a few miles east of the Oracle junction.

Total, 8: 10 m. N Tucson, 2800 ft., 1 (BS); Oracle, 6 (BS); 1 m. S Oracle, 1 (UA).

39. *Dipodomys merriami merriami* Mearns.—This is the common kangaroo rat in the lower desert, ranging from the shrubby flats to the grasslands. Doutt (1934: 263) found the nocturnally active Merriam kangaroo rat in the same habitats as the diurnally active Harris ground squirrel.

Total, 73: Ft. Lowell, 25 (USNM); Santa Catalina Mt. foothills, S face, 2400-3000 ft., 43 (35, UA; 4, Carnegie; 3, KU; 1, UM); 3 m. S, 4 m. W Oracle, 1 (UA); 1 m. S Oracle, 4500 ft., 2 (UA); 6 m. ESE Oracle, 2 (UA).

40. *Dipodomys ordii ordii* Woodhouse.—Setzer (1949: 532) reports three Ord kangaroo rats collected at Fort Lowell. Dice took one in catclaws and mesquites (*Acacia* and *Prosopis*) southeast of Oracle (Dice and Blossom, 1937: 31).

Total, 8: Ft. Lowell, 3 (D.R.D.); Oracle, 4 (BS); 6 m. SE Oracle, 1 (UM).

41. *Castor canadensis* ssp.—Beaver were apparently introduced in Upper Sabino Canyon, Marshall Gulch, 7600 feet, in the early 1930's. There may have been later introductions. The following is an extract from the journal of D. J. T. Marshall, dated May 19, 1951: "Marshall Gulch, Catalina Mts., Arizona. At 10 AM starting down Sabino Canyon following creek . . . Beaver sign incr. got fresher

all way until into fresh droppings, dams, houses, cut willow twigs, cut greenery of white fir to plug dams, etc. — this about 4 or 5 miles down." Jackson (1954: 3) notes: "Streams found to contain beavers include . . . Sabino Canyon Creek . . . None of the areas were found to contain appreciable numbers of beavers." The author knows of no reliable records of beaver in the Catalinas in recent years.

42. *Onychomys torridus torridus* (Coues).—The southern grasshopper mouse has been taken in mesquite-grassland (Dice and Blossom, 1937: 32) and in desert shrub habitats. "This form appears to be abundant south of the Mogollon Mesa wherever there are sandy mesquite covered plains and river-bottoms. We found it abundant at Fort Lowell." (Price, *in* Allen, 1895: 225).

Total, 28: Ft. Lowell, 14 (USNM); Santa Catalina Mt. foothills, S face, 2400-2700 ft., 3 (UA); 2 m. E Oracle jct., Pinal Co., 4 (UA); Oracle, 4 (3, BS; 1, UM); 3 m. E Oracle, 1 (UA); 6 m. SE Oracle, 4400 ft., 2, (UA).

43. *Reithrodontomys megalotis megalotis* (Baird).—The western harvest mouse is represented by only one specimen, taken in 1923. Dice, in 1932, secured a specimen five miles north of Oracle in paloverde, mesquite, and grass (Dice and Blossom, 1937: 32).

Total, 1: 2 m. E Ft. Lowell (BS).

44. *Peromyscus maniculatus sonoriensis* (Le Conte).—This lowlands form has been collected in grassy areas on both sides of the mountains. It has been taken in the same trap-line with *P. eremicus* and *P. boylei* at Molino Basin on the south face of the mountains. This area along the Mt. Lemmon highway is in the Upper Desert Slopes zone of Shreve (1915). The vegetation consists of scattered oaks and mesquites; ocotillos and agaves; shrubs, mainly *Aplopappus, Baccharis* and *Asclepias;* and grasses. The ground cover, which is much more extensive than in the bahadas, is broken along the creek by rocks and boulders. At 4200 feet, this area represents the lower limits of *P. boylei* and the upper limits of *P. eremicus. P. m. sonoriensis* and the following subspecies are apparently separated by the oak and pinyon-juniper vegetation.

Total, 7: Molino Basin, 4200 ft., 3 (UA); Oracle, 2 (BS); Linda Vista Ranch, 2½ m. S Oracle, 1 (UA); 10 m. SE Oracle, Pinal Co., 4600 ft., 1 (UM).

45. *Peromyscus maniculatus rufinus* (Merriam).—The tawny deer mouse is common in the higher elevations. Dice and Blossom (1937: 34) found them more common in the Douglas firs than in the ponderosa pine.

Total, 74: Summerhaven, 7500-7600 ft., 27 (25, UM; 2, BS); Carter Canyon, 7600 ft., 1 (UA); Soldier Camp, 7 (6, Carnegie; 1, MVZ); N slope Mt. Lemmon, 8000-8600 ft., 38 (UM); N slope Mt. Lemmon, 8800 ft., 1 (UA).

46. *Peromyscus boylei rowleyi* (J. A. Allen).—Doutt (1934: 265) and Dice and Blossom (1937: 35) noted the brush mouse in wooded areas from the lower oaks to the firs. Dice and Blossom

(1937: 36) found it most abundant in the encinal, and thought that this was related to the animal's semi-arboreal nature.

Total, 98: Santa Catalina Mts., 8 (BS); Molino Basin, 4200 ft., 20 (10, UA; 10, KU); Oracle, 1 (BS); 1½ m. S Oracle, 4500 ft., 2 (UA); 5-8 m. SE Oracle, Pinal Co., 26 (13, UA; 7, UM; 6, MVZ); Santa Catalina Mts., rocky hillside, 5200 ft., 2 (UA); Santa Catalina Mts., N base, 5500 ft., 1 (BS); Santa Catalina Mts., N slope, 5600 ft., 2 (UM); near Soldier Camp, 3 (Carnegie); Summerhaven, 34 (31, UM; 2, UA; 1, BS); Mt. Lemmon, N slope, 8550 ft., 1 (UM).

47. *Peromyscus eremicus eremicus* (Baird).—The cactus mouse ranges from the lowest limits of the study area to about 4300 feet on the south face and 4700 feet on the north face.

Total, 111: Ft. Lowell, 15 (8, UM; 4, BS; 3, USNM); Santa Catalina Mt. foothills, S face, 24-3000 ft., 45 (32, UA; 12, UM; 1, KU); Upper Sabino Canyon, 3200 ft., 4 (UA); Finger Rock Canyon, 3200 ft., 1 (UA); Pima Canyon, 3500 ft., 2 (BS); 3 m. N, ½ m. E Redington, 2 (UA); 2 m. S, 1½ m. W Redington, 4000 ft., 10 (UA); Molino Basin, 4200 ft., 7 (UA); 1 m. W, 1 m. S Oracle, 1 (UA); Linda Vista Ranch, 2½ m. S Oracle, 1 (UA); 6-8 m. SE Oracle, Pinal Co., 23 (21, UM; 2, UA).

48. *Peromyscus leucopus arizonae* (J. A. Allen).—This form has been taken on both sides of the Catalinas, but apparently is rare.

Total, 4: Ft. Lowell, 2 (1, BS; 1, USNM); 4¾ m. S, 3 m. E Oracle, Pinal Co., 4600 ft., 2 (UA).

49. *Sigmodon hispidus cienegae* A. B. Howell.—The type locality of *Sigmodon hispidus cienegae* is Bullock's Ranch, four miles east of Fort Lowell (Miller and Kellogg, 1955: 525). The hispid cotton rat has been collected in the following localities: along Rillito Wash; Binghampton pond; a cattail (*Typha*) marsh in Lower Sabino Canyon; in grass along a fence row at the University of Arizona Farm; and along a dry wash in *Prosopis* and *Opuntia* growth.

Total, 12: Ft. Lowell, Rillito Wash, 2 (UM); Binghampton pond, 7 m. NE Tucson, 4 (3, UA; 1, MVZ); Univ. Ariz. Farm, 1 (UA); Lower Sabino Canyon, 3 (UA); 20 m. N Tucson, Pinal Co., 1 (UA); 2 m. E Oracle jct., 1 (UA).

50. *Neotoma albigula albigula* Hartley.—The type locality of *Neotoma albigula albigula* is in the vicinity of Fort Lowell (Miller and Kellogg, 1955: 535). Price found the white-throated woodrat abundant by Fort Lowell, ". . . having numerous nests among cactus beds, brush fences, and in willows along the Rillito." (*in* Allen, 1895: 223). It is common in the grasslands of the north face (Dice and Blossom, 1937: 38). None have been taken in ponderosa pine, but one has been collected in encinal on the north face.

Total, 91: Ft. Lowell, 12 (6, MVZ; 4, BS; 2, USNM); near Ft. Lowell, 17 (11, MVZ; 5, BS; 1, UM); Santa Catalina Mt. foothills, S face, 2400-3000 ft., 13 (9, UA; 2, UM; 2, KU); Pima Canyon, 3500 ft., 3 (BS); Reddington Pass, 24 m. E Tucson, 1 (UA); near Redington, 2 (UA); Molino Basin, 4200 ft., 7 (UA); Oracle, 6 (5, BS; 1, SDSNH); 1½-2½ m. SW

Oracle, 3 (UA); 3-10 m. SE Oracle, Pinal Co., 26 (UM); Santa Catalina Mts., N base, 5500 ft., 1 (BS).

51. *Neotoma mexicana bullata* Merriam.—This race of the Mexican woodrat is known only from the Catalina Mountains, where it is confined to the higher elevations. Dice found nests around boulders on ponderosa pine slopes and noted one animal in oak brush near Summerhaven (Dice and Blossom, 1937: 39).

Total, 20: Summerhaven, 16 (7, UM; 5, BS; 3, UA; 1, SDSNH); Carter Canyon, 3 (UA); ½ m. SE Soldier Camp, 7900 ft., 1 (Carnegie).

52. *Mus musculus* ssp. Total, 4: near Ft. Lowell, 3 (2, BS; 1, UM); Molino Basin, 4200 ft., 1 (UA).

53. *Rattus norvegicus norvegicus* (Berkenhout).— Total, 1: Ft. Lowell (USNM).

54. *Erethizon dorsatum couesi* Mearns.—Porcupines have been seen near Rillito Wash on Sabino Canyon Road, in the Catalina foothills (near Campbell Avenue and East River Road), and in Upper Sabino Canyon (about 3200 feet). The observations and comments of Reynolds (1957) are of interest here. Taylor's finding (1935: 103) that pinyon pine is apparently relished by porcupines may indicate that *Erethizon* spends considerable time in this vegetative type. Other records are as follows: a road-kill on the Mt. Lemmon highway two miles above the prison, and a specimen taken on the north face just below the top by predator control agents. Indications are that *E. d. couesi* has a wide tolerance and adaptability in the Catalinas.

55. *Euarctos americanus amblyceps* (Baird).—Vernon Bailey (1889) reported bear tracks "near the summit and along the streams." The *Arizona Daily Star,* in 1898, reported that: "Ed Johnson and family, who have been camped on Mt. Lemmon for some time, have been heard from . . . it is reported they have killed ten bears, eight mountain lions, 17 wolves. . . ." A few black bears still inhabit the higher elevations. Gerald I. Day reported a July 1956 sight record by Harold Lim near Summerhaven. This bear was observed at night in a refuse area. Boy scouts at Camp Lawton, Mt. Lemmon, made a cast of a black bear track near Summerhaven in July 1956 (L. R. Commissaris, personal communication). Forest Service personnel have sighted black bear in the Catalinas, but not in recent years.

56. *Procyon lotor mexicanus* Baird.—Price (*in* Allen, 1895: 250) said this of the raccoon: ". . . common in willow thickets along the Rillito Creek at Fort Lowell." Sight records and reports indicate that *P. l. mexicanus* is most common in picnic and resort areas, particularly Sabino Canyon and Summerhaven. These areas are located near streams, where the raccoon may secure water and additional food.

Total, 4: Ft. Lowell, 2 (USNM); Sabino Canyon, 1 (BS); Summerhaven, 1 (UM).

57. *Nasua narica molaris* Merriam.—The coati-mundi is herein reported from the Santa Catalina Mountains for the first time on the basis of the following records: (1) William J. Schaldach, Jr., reported sighting one in the ponderosa pines near Summerhaven and six in Upper Sabino Basin in 1945; and (2) C. Roger Hungerford reported *Nasua* tracks in a dry wash near the Old Desert School, about ten miles north of Tucson, in *Simmondsia-Carnegia* habitat, in 1956. Coati-mundis have now been reported from the following mountain ranges in southeastern Arizona: Santa Catalinas, Huachucas, Chiricahuas, Patagonias, Santa Ritas, and Tumacacoris (Taber, 1940: 13).

58. *Bassariscus astutus arizonensis* Goldman.—Ringtail cats range from the lowest to the highest limits of the study area. Like raccoons, they seem to be most common in picnic and resort areas, particularly those with streams flanked by rocky hillsides. Summerhaven residents report them coming into their attics. Ringtails undoubtedly range at times from Summerhaven and Soldier Camp into the firs at higher elevations.

Total, 5: edge of Tucson, 1 (UA); 16 m. E Tucson on Tanque Verde Rd., 1 (UA); Ft. Lowell, 3 (A. B. Howell).

59. *Spilogale putorius leucoparia* Merriam.—This species and the three reported below are probably sympatric at the lower elevations of Sabino Canyon. The following records from Sabino Canyon are the author's: sight and specimen records for *Spilogale;* sight, and trap and release records for *Mephitis mephitis;* and sight records for *Conepatus.* In addition, *Mephitis macroura* has been taken at Fort Lowell and probably inhabits the lower elevations of Sabino Canyon as well. The relationships of this distributional pattern would be an interesting and revealing study.

Total, 10: Ft. Lowell, 1 (USNM); Lower Sabino Canyon, 2 (UA); Sabino Canyon, 1 (USNM); Molino Basin, 20 m. NE Tucson, 1 (UA); Stratton Mine, Santa Catalina Mts., 1 (Carnegie); near Soldier Camp, 4 (Carnegie).

60. *Mephitis mephitis estor* Merriam.—Total, 7: Ft. Lowell, 3 (USNM); near Soldier Camp, 2 (Carnegie); near Summerhaven, 1 (UA); Carter Canyon, 7600 ft., 1 (UA).

61. *Mephitis macroura milleri* Mearns.—The hooded skunk has been collected in the study area only at the type locality, Fort Lowell. Total, 3: Ft. Lowell (2, MVZ; 1, BS).

62. *Conepatus mesoleucus venaticus* Goldman.—Collection and sight records are from the lower elevations. Dice and Blossom (1937: 19) report forest ranger observations at the higher elevations. Total, 3: Vicinity of Ft. Lowell, 1 (MVZ); mouth Sabino Canyon, 6 m. N, 10 m. E Tucson, 1 (KU); Sabino Canyon, 17 m. NE Tucson, 1 (UA).

63. *Taxidea taxus berlandieri* Baird.—Price regarded the badger as common in the plains region (*in* Allen, 1895). The author has

seen a badger in gravelly soil at 4200 feet elevation on the north face just below Reddington Pass in the following vegetation: scattered mesquites, acacias, oaks, ocotillos, *Aplopappus,* and grasses.

Total, 3: Ft. Lowell, 2 (1, BS; 1, Stanford); Peppersauce Canyon, 1 (Carnegie).

64. *Vulpes macrotis arsipus* Elliot.—The following is part of a letter from C. E. Gillham to W. P. Taylor, dated April 19, 1934: "As far as I know from personal trapping and observation of other trappers, the swift fox is found to some extent in practically all the desert areas, probably from the San Pedro River west and on into California in the sand dune country . . . and they are found to some extent on practically all the desert range south, you might say, of the oak country in what would be usually the true desert type of Arizona. It seems to me one usually finds swift fox most abundant where the nature of the desert is sandy rather than rocky. Probably either his own burrowing tendencies or the desire for burrowing for rodents may have something to do with this." Records from the Catalinas confirm Gillham's observations: the swift fox is most common in the shrubby desert flats and the foothill country. Trapping and poisoning campaigns have greatly reduced their numbers.

65. *Urocyon cineroargenteus scottii* Mearns. — The gray fox seems to be most common in the foothills and canyon mouths, but it also occurs in the pines and firs. Taylor (1924) found *Juniperus pachypholoea* fruits almost exclusively in gray fox droppings collected in Sabino Canyon below the Basin. Dice and Blossom (1937: 19) noted what were probably gray fox feces on a ponderosa pine slope. These droppings contained rock squirrel and woodrat hair. The diet may vary with the habitat and with the season.

Total, 14: Ft. Lowell, 8 (A. B. Howell); Tanque Verde, 1 (KU); Santa Catalina Mts., 4 (BS); mouth Sabino Canyon, 6 m. N, 10 m. E Tucson, 1 (KU).

66. *Canis latrans mearnsi* Merriam.—Coyotes have been heard in Peppersauce Canyon, about eight miles southeast of Oracle (Dice and Blossom, 1937: 20), and at Summerhaven. Their preferred habitat or area of greatest concentration may be in the lower elevations.

Total, 3: Santa Catalina Mts., 1 (Carnegie); Ft. Lowell, 1 (DRD); 25 m. N Tucson, 1 (Carnegie).

67. *Canis lupus baileyi* Mearns.—The *Arizona Daily Star,* in 1898, reported that: "Ed Johnson and family, who have been camped on Mt. Lemmon for some time, have been heard from . . . it is reported they have killed . . . 17 wolves. . . ." The following is an extract of a letter, dated November 28, 1956, from Everett M. Mercer to the author: "During April of 1937, I spent three days hunting lions . . . in the Santa Catalina Mountains. We saw the tracks of a large wolf during the second day that we were there, and we followed it for two

or three miles. It came out on top of the mountain and drifted off to the east toward the San Pedro River." A Pittman-Robertson hunter employed by the Game Department took a wolf in July, 1948, in the Catalinas (Mercer, 1949: 6). Pierre Early, a reliable observer, has reported the following to me, in a letter dated August 18, 1958: "About the Mex. Lobos. the first sight of them would have been in October 1955 — one carrying uneaten portion of a large yearling whitetail. Second sighting about March or April 1956 — the pair sighted near our dump grounds. Sign has been seen several times since." The locality is the mouth of Sabino Canyon, elevation 3000 feet.

68. *Felis concolor azteca* Merriam.—Mountain lions inhabit the higher elevations. Annual game population estimates for the Santa Catalina District, Coronado National Forest, run from 10 to 18 animals for the period, 1937 to 1948. Doutt (1935) reports sight records near Soldier Camp. Dice and Blossom (1937: 20) report that one cougar was killed in 1932 near Soldier Camp. Mountain lion sign has been found in the Mt. Lemmon, Upper Sabino, and Stratton Mine areas (Knipe, 1951). Total, 1: Santa Catalina Mts., Pinal Co. (UA).

69. *Lynx rufus baileyi* Merriam.—Bobcats, like most of the larger predators in the Catalinas, range from the desert flats to the pines and firs. The preferred habitat, if any, is not known. Annual game population estimates for the Santa Catalina District, Coronado National Forest, range from 400 to 550 animals for the period, 1937 to 1948. Total, 1: Ft. Lowell (BS).

70. *Tayassu tajacu sonoriensis* (Mearns).--Although javelina are most common in desert shrub habitat, such as *Simmondsia,* they have been seen in ponderosa pine at an elevation of 6700 feet (Reed, 1956) and in oak and ponderosa pine on the east side and in the Canada del Oro country (Knipe, 1953). Some indication of population size in the study area is given by the following hunt kills, gathered and compiled by personnel of the Arizona Game and Fish Department: 1952, 76; 1953, 88; 1954, 80; 1955, 138; and 1956, 90. Total, 1: Santa Catalina Mts. (MVZ).

71. *Odocoileus virginianus couesi* (Coues and Yarrow).—Coues deer range from the flats to the summits. The author has seen them in Lower Sabino Canyon, elevation 3000 feet, in September. They usually range above mule deer, however, and are most common in the higher elevations. Total, 3: Santa Catalina Mts., 1 (USNM); 2 m. SE Soldier Camp, 1 (Carnegie); Summerhaven, 1 (UM).

72. *Odocoileus hemionus crooki* (Mearns).—Mule deer range through the desert shrubs in the flats and foothills on the south face, and through the desert grasses and shrubs on the north face. Price (*in* Allen, 1895) found them in foothills and ravines of the lower mountain ranges and thought that they preferred open country with oak woods.

73. *Ovis canadensis mexicana* Merriam.—The Catalina bighorns have been mentioned by many writers, among them the following: "In the year 1885 I ascertained that mountain sheep occurred in the . . . Santa Catalina mountains. . . ." Mearns (1907: 239); "Not uncommon on the bare rocky spurs of the Santa Catalina Mountains, where they were seen during 1894. Several were killed in the fall of 1893 by an Indian hunter, and the meat sold to settlers at the foot of the mountains. . . ." Price (*in* Allen, 1895: 258); and Hornaday (1908: 341-42). Fred Winn, Coronado National Forest supervisor, stated in the *Tuscon Citizen* (anonymous, 1928) that the most recent game census estimated 220 sheep in the Catalinas and that this population was the largest in the state. The 1937 census estimated 80 sheep from fresh sign and actual sightings (Bogar, 1956). Poaching, drought, and the development of roads caused continual decline in the Catalina bighorn population (Bogar, 1956). Knipe (1951) saw six animals and estimated the number at 35; Reed (1956) thought that the maximum number was 15, with the probable number between six and ten.

Total, 2 (3?): Santa Catalina Mts., 1 (UA); near Old Sutherland Ranch, Canada del Oro, 1 (BS); Santa Catalina Mts. or some near-by range, 1 (BS).

Hypothetical and Extinct Species

1. *Sylvilagus floridanus holzneri* (Mearns).—This species generally ranges from the lower encinal into the ponderosa pines in those mountains of southern Arizona where it has been found (Sowls, 1957: 235). Local residents have reported a large cottontail from the Catalinas (Dice and Blossom, 1937: 43); it seems likely that this form is found in the oaks and pines of the Catalinas.

2. *Ursus* sp. (*U. arctos* L. ?).—It seems likely that grizzlies formerly occurred in the Catalinas, but their date of extinction is not known. The only references appear to be the following: (1) Vernon Bailey (1889): "The grizzly is here called the Silver-tip Bear. They are said to be common. I saw a number of bear tracks high up in the mts. and one very large track that must have been made by a Grizzly. Other smaller tracks were probably of Black or Brown Bears. Most of the tracks were near the summit and along the streams." (2) M. E. Musgrave, in a letter dated June 7, 1921: "We also have another grizzly that ranges in the Rincon Mountains, north of Tucson."

3. *Felis yaguarondi tolteca* Thomas.—Little (1938) reports sighting a jaguarundi in Santa Cruz County, Arizona, on March 17, 1938. This appears to be the only record of this subspecies in the United States up to the present time, with the following possible exceptions. Peterson and Fisher (1955: 236) record this observation along the Sabino Canyon Road: ". . . a black cat padded across bone-dry Pantano Wash . . . the black form of the jaguarundi. . . . We had the privilege of glimpsing this little-known cat in a part of its range where

it is very rare." The author has a sight record of "a stocky, long-tailed, cat-like animal" in Upper Sabino Canyon, 3200 feet, on November 16, 1956, but in consideration of the brevity of observation and the rarity of the animal involved, he mentions it merely for possible future significance.

4. *Felis onca arizonensis* Goldman.—Nelson and Goldman (1933: 237) give the range of this subspecies of the jaguar as the mountainous regions of eastern Arizona, southwestern New Mexico, and northeastern Sonora, Mexico. Jaguars occasionally passed through the Catalinas and apparently still occur in southern Arizona. Herbert Brown (*in* Hock, 1955: 325) referred to a jaguar-kill in the Rincon Mountains in 1902. C. T. Vorhies (*in* Seton, 1929: 11) reported that one was taken in the Catalinas around 1912, and one was killed in the adjacent Rincon Mountains in 1912. E. A. Goldman saw the skin of a jaguar taken in the Tortolito Mountains, about 30 miles northwest of Tucson, in 1913. The Holbrook *Observer* of January 20, 1920, reported a jaguar killed in the Rincon Mountains, Pima County, "on Saturday." One was seen in September, 1920, about three miles northwest of Tucson in Pima County along the Silverbell Highway. The animal was traveling east, towards the Santa Catalina Mountains (Vorhies, *in* Seton, 1929: 10). E. A. Goldman, in memorandums dated July 17-18 and August 4-9, 1923 reported that: "A man named Al James is said to have seen a jaguar that killed one of his burrows near Mt. Lemmon about July 1st."

5. *Felis pardalis sonoriensis* Goldman.—Goldman (1943: 378) gives the range of the subspecies *sonoriensis* as the west slopes of the Sierra Madre, northward from southern Sonora to southeastern Arizona, formerly west to Fort Verde in Yavaipai County, Arizona. It is possible that ocelots formerly passed through the Catalinas.

6. *Antilocapra americana* ssp.—The pronghorn antelope was known from the study area until some 30 years ago. The following records are pertinent: (1) W. P. Taylor (1925), referring to the Oracle Plains: "Stanley Kitt, a long time resident of Tucson, says he remembers seeing bands of 20 to 40 antelope. . . . This was in the 80's."; (2) Vernon Bailey (1889), referring to Oracle: "Said to be a few in the valley below here."; (3) A. K. Fisher (1892): "Mr. Herbert Brown saw a band of twenty or more near Tucson in the spring."; (4) E. A. Goldman (1923), referring to the road to Florence, 35 miles northwest of Tucson: "J. H. Durham, an old cattle man familar with game conditions, reports having seen 5 antelope . . . in June of this year."

The following are included in the hypothetical list on the basis of their known distribution in Arizona:

7. *Sorex merriami leucogenys,* higher elevations(?)

8. *Mormoops megalophylla,* oaks (?)

9. *Leptonycteris nivalis,* oaks (?)
10. *Myotis occultus*
11. *Myotis evotis*
12. *Lasionycteris noctivigans,* higher elevations in summer (?)
13. *Tadarida molossa*
14. *Perognathus longimembrus*
15. *Perognathus hispidus*
16. *Reithrodontomys montanus,* grasslands on north face (?)
17. *Reithrodontomys fulvescens*
18. *Peromyscus merriami,* mesquite bosques and washes (?)
19. *Sigmodon minimus,* oaks (?)

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The Genitalia of the Buffalo Treehopper, *Stictocephala bubalus* (Fabricius)

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Genital morphology is often used as a basis of insect taxonomy. To be useful, a taxonomic character must be constant and unique. In theory, the genital structures should be constant within each species. The purpose of this study has been to determine the degree of constancy or variability in the genitalia of both sexes of the buffalo treehopper, *Stictocephala bubalus* (Fabricius).

Acknowledgments.—Several people and institutions have been very helpful during this study and to them I wish to express my grateful appreciation.

Specimens for study were obtained from the following: Warren T. Atyeo, University of Nebraska; W. F. Barr, University of Idaho; William E. Bickley, University of Maryland; A. R. Brooks, University of Saskatchewan; Paul P. Burbutis, University of Delaware; George W. Byers, University of Kansas; Leland Chandler, Purdue University; J. F. Gates Clarke, Smithsonian Institution; P. J. Darlington, Jr., Harvard College; Henry Dietrich, Cornell University; William A. Drew, Oklahoma State University; Roland L. Fischer, Michigan State University; Leonora K. Gloyd, Illinois Natural History Survey; Frank F. Hasbrouck, Oregon State College; Cluff Hopla, Oklahoma University; Ross Hutchins, Mississippi State University; Josef N. Knull, Ohio State University; Jean L. Laffoon, Iowa State University; John W. McReynolds, Nevada, Missouri; Norman L. Marston, Kansas State University; Frank W. Mead, North Carolina State College; John Medler, University of Wisconsin; J. R. Millar, Chicago Natural History Museum; D. H. Pengelly, Ontario Agricultural College; R. E. Pfadt, University of Wyoming; Roy W. Rings, Ohio Agricultural Experiment Station, Wooster; A. G. Robinson, University of Manitoba; Herbert Ruckes, American Museum of Natural History; G. G. E. Scudder, University of British Columbia; Frank R. Shaw, University of Massachusetts; Roy Shenefelt, University of Wisconsin; Vasco M. Tanner, Brigham Young University; and Ruth Williams, Entomological Research Institute, Ottawa. T. J. McKnight and Sherry Roseberry, East Central State College, provided valuable assistance. This work was supported in part by a grant from Frontiers of Science Foundation of Oklahoma, Inc.

Procedure

Specimens of both sexes were secured from the greater part of the range of this species in North America. A total of 2021 specimens (consisting of 1009 males, 1009 females and 3 with features of both sexes) from 39 states, the District of Columbia and 7 Canadian provinces were examined.

The abdomens were cleared in 10 per cent potassium hydroxide solution, washed in water and stored in corked 10 x 25 mm vials in glycerine. The vials were pinned separately, and corresponding numbers were attached to the specimen pins and the vial pins. Examination and dissection were carried out under glycerine in a spot plate.

The terminology employed is that which I used in an earlier paper (Dennis, 1952).

General Description of the Genitalia

male

The male parts are illustrated in Figures 1-6. The dorsal abdominal tergite IX, the lateral valves and the ventral subgenital plate enclose the aedeagus, the styles and the connective. Abdominal tergites X and XI form the anal tube.

The lateral valves each have a single broad, blunt tooth. The subgenital plate is broadly rounded at its base and narrowed in the distal half; the distal margin has a small acute notch.

The anterior arm of the aedeagus articulates with the base of the anal tube. Ventrally, the aedeagus is lobed at its articulation with the connective. The posterior arm of the aedeagus has lateral membranes which meet below the middle of its anterior face. In the middle of the posterior face of the posterior arm is the functional orifice which is rounded below, acute above and equals two-thirds of the height of the arm. The aedeagus is the penis sheath.

The connective is elliptical except for a shallow, rounded notch in its anterior margin. Its sides are folded dorsally so that it appears V- or U-shaped when viewed from the end.

The styles articulate laterally with the connective. The point of articulation of the styles and the connective is the dividing point between the anterior and posterior arms of these structures. The anterior arms are roughly cylindrical, divergent and with no distinctive features. The posterior arms are upturned distally, almost straight in dorsal aspect and acuminate at their tips. On the outer margin of each posterior arm is a row of short hairs on the distal two-thirds; the inner margin has a similar row on the distal half to third. The styles are used as claspers during copulation.

variation in the male

Abdominal tergites IX, X and XI—These structures exhibit no significant variation.

Subgenital plate.—The subgenital plates are also rather constant and have the form illustrated in Figure 2. One specimen from South Dakota has the posterior notch extended as a split reaching one-third of the way to the base (Fig. 7).

Lateral valve.—The valves themselves have practically no variability in form, but the teeth do show a few variations. The typical form of the tooth is shown in Figure 4. Most variations are very slight and of little significance. Nine specimens have teeth which are noticeably narrower than the typical form (Fig. 8). The narrow teeth were found on one specimen which was collected in Wisconsin, one from Washington, two from Ontario, two from Iowa and three from Michigan. A specimen from Wyoming has blunt teeth (Fig. 9).

Two treehoppers, one from Kansas and one from Oklahoma, have a slight ventral sinuation near the tip of the tooth (Fig. 10). One specimen from British Columbia has a narrow tooth on the left valve and a typical tooth on the right valve.

Connective.—No significant variations were found in the connectives; they all appear as is shown in Figure 3.

Styles.—The styles are rather constant, exhibiting only very slight variations. A typical style is illustrated in Figures 1 and 3. The only noticeable variation is a small dorsal notch at the tip of the right style of a single Maryland specimen (Fig. 11). A few styles appeared to be very slightly curved inward at the tips.

Aedeagus.—The anterior arm shows considerable variability; the posterior arm is much more constant in form but still has some slight variations. What is considered to be the typical form is illustrated in Figures 5 and 6.

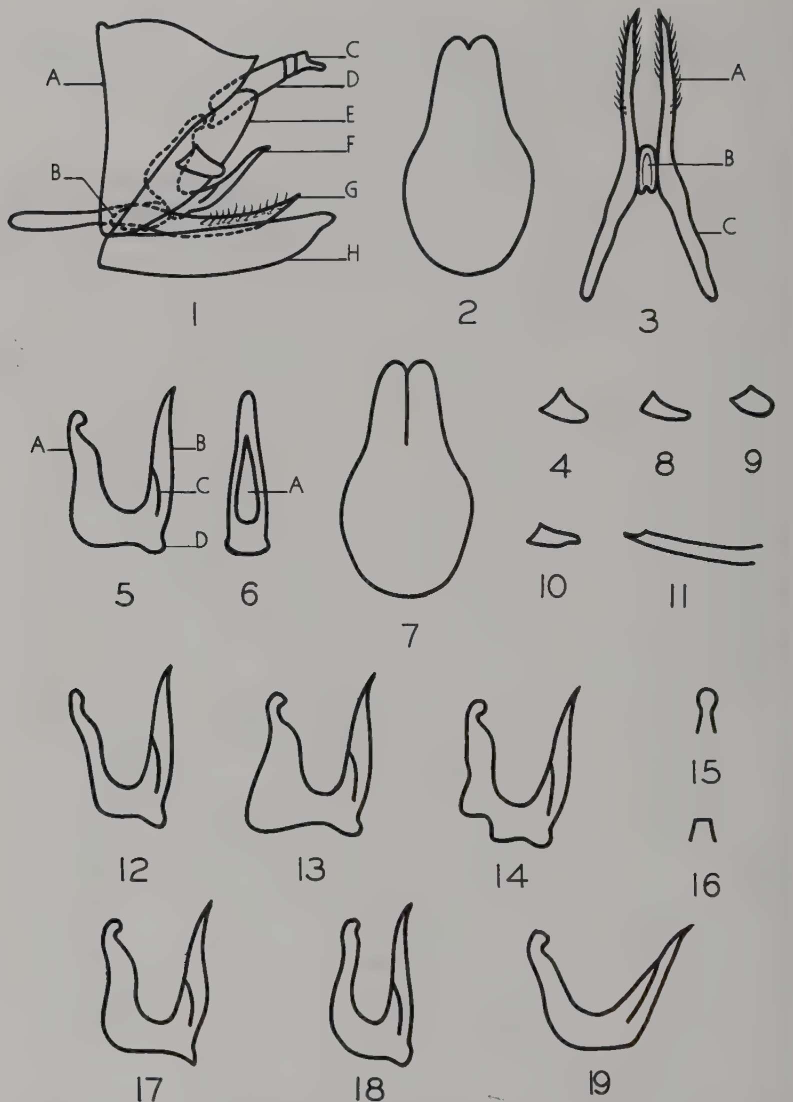
It is difficult to classify the variations of the anterior arm because there are many intergradations. The most common variation is a rather slender anterior arm (Fig. 12), found in 121 specimens. Of these, 71 have normally sclerotized genitalia and abdomens; in the remaining 50, these structures are weakly sclerotized. The anteroventral part of this arm is rather bulbous in 33 specimens and is broadly notched in 35 specimens. These two variations are illustrated in Figures 13 and 14, respectively. It should be kept in mind that this arrangement of the variations into three groups is a very arbitrary one and that actually much intergradation exists. No geographic correlation could be made with respect to variations in the anterior arm of the aedeagus.

The posterior arm is rather constant. Ten specimens, six from Michigan, three from Alberta and one from Iowa, have the definitely expanded tip when viewed in posterior aspect (Fig. 15). Fifteen specimens have the posterior arm truncate at the tip when seen in posterior aspect (Fig. 16). Four of these are from South Dakota, ten from Kansas and one from Washington. Several aedeagi show gradations between these variations of the tip and the more typical form. In some specimens the posterior arm appears to be slightly more slender and slightly more erect than the typical form. This, again, is a matter of degree and is not considered to be significant. No particular variation was noted in the position or form of the lateral membranes or the functional orifice.

The ventral lobe of the aedeagus shows a few minor variations in form. The only striking variation is in two specimens, one from Iowa and one from Wyoming, which have an acute lobe when viewed from the side (Fig. 17).

One specimen from New York and one from Maryland have the two arms of the aedeagus closer together than usual (Fig. 18).

Two specimens, one from Wyoming and one from Michigan, have the anterior arm and the posterior arm distinctly more divergent than usual (Fig. 19).



Figs. 1-19. Male genitalia. 1. Terminalia, left lateral view; A, Tergite IX; B. Connective; C. Tergite XI; D. Tergite X; E. Lateral valve; F. Aedeagus; G. Style; H. Subgenital plate. 2. Subgenital plate, ventral, posterior margin up. 3. Styles and connective, dorsal; A. Style, posterior arm; B. Connective; C. Style, anterior arm. 4. Tooth of lateral valve, usual form. 5. Aedeagus, lateral; A. Anterior arm; B. Posterior arm; C. Lateral membrane; D. Ventral lobe. 6. Aedeagus, posterior; A. Functional orifice. 7. Subgenital plate, South Dakota specimen. 8-10. Tooth of lateral valve. 8. Narrow form. 9. Wyoming specimen.

FEMALE

Figures 20-23 illustrate the female parts. Abdominal tergite IX, sternite VII and valvulae 1 and 3 enclose valvula 2 and the valvifers. The anal tube is composed of tergites X and XI.

Sternite VII is truncate basally and slightly rounded on the sides. Its posterior margin is a subacute-bottomed notch with broadly sinuate sides reaching half the depth of the sternite.

The two valvulae 1 have the tips narrowed, sinuate above and below, with transverse ridges extending below the ventral margin. The one valvula 2 typically has a single tooth somewhat removed from the coarse dorsal serrations before the tip. Valvula 2 is closed dorsally to the single tooth, open from the single tooth to the tip and ventrally. The base of valvula 2 is bifurcate with the arms curving upward. The two valvulae 3 are narrow in the basal half and then rather abruptly broadened dorsally and tapered to the rounded tip; the broadened part is somewhat spoonshaped.

Near the bases of the inner aspect of tergite IX are condyles which articulate with the two second valvifers. These valvifers articulate posteriorly with valvulae 3 and anteriorly with the arms at the base of valvula 2. The two first valvifers join the bases of valvulae 1. Valvulae 1 and laterally connected with valvula 2 by tongue-and groove sliding joints.

Valvula 2 is the ovipositor proper. It slides on valvulae 1 in a saw-like motion as the eggs are inserted under the bark of twigs. The dorsal teeth before the tip aid in cutting bark.

VARIATION IN THE FEMALE

Abdominal tergites IX, X and XI—.These tergites show no significant variation.

Abdominal sternite VII.—This structure is rather constant and has the form illustrated in Figure 23. One Maryland specimen has a rather shallow notch on the posterior margin (Fig. 24). One from Washington has a similar posterior margin, but not quite as shallow (Fig. 25).

Valvifers 1 and 2.—No significant variations were found in the valvifers.

Valvulae 1 and 3.—These valvulae exhibit no particular variations.

Valvula 2.—Some variability was found in valvula 2. The tip of the typical form is shown in Figure 21. The most common variation is the presence of a tiny tooth between the single tooth and the coarse serrations (Fig. 26). This was found on 58 females collected throughout the range of this species. The position of this tiny tooth

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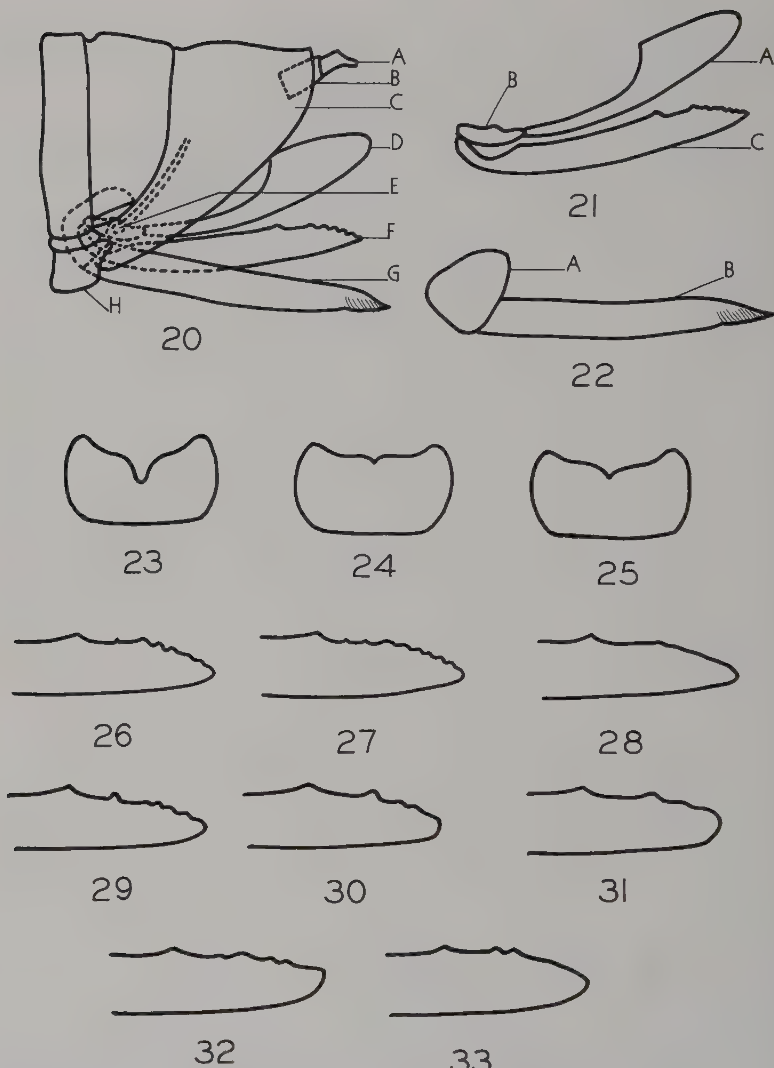
10. Kansas and Oklahoma specimens. 11. Style, right lateral, Maryland specimen. 12-19. Aedeagus. 12. Lateral, slender anterior arm. 13. Lateral, bulbous antero-ventral part. 14. Lateral, broadly notched antero-ventral part. 15. Tip, posterior, expanded. 16. Tip, posterior, truncate. 17. Lateral, acute ventral lobe. 18. Lateral, arms close together. 19. Lateral, arms divergent.



Figs. 20-33.—Female genitalia. 20. Terminalia, left lateral view; A. Tergite XI; B. Tergite X; C. Tergite IX; D. Valvula 3; E. Condyle; F. Valvula 2; G. Valvula 1; H. Sternite VII. 21. Valvulae 2, 3, valvifer 2, left lateral; A. Valvula 3; B. Valvifer 2; C. Valvula 2. 22. Valvula 1, valvifer 1, left lateral; A. Valvifer 1; B. Valvula 1. 23-25. Sternite VII, ventral, posterior margin up. 23. Usual form. 24. Maryland specimen. 25. Washington specimen. 26-33. Valvula 2, variations of tip, left lateral. 26. Tiny tooth between single tooth and serrations. 27. Two tiny teeth between single tooth and serrations. 28. Obscure serrations. 29. Colorado specimen. 30. Pennsylvania specimen. 31. Indiana specimen. 32. Wisconsin specimen. 33. Massachusetts specimen.

is not uniform; it was found at various positions between the single tooth and the serrations. Four specimens, one from New Jersey, one from Kansas and two from Nebraska, have two tiny teeth between the single tooth and the serrations (Fig. 27).

Rather obscure serrations are present on 16 specimens from widely scattered localities (Fig. 28). Four of these from Iowa also have weakly sclerotized abdomens. Five other variations in tips which occurred on single specimens from Colorado, Pennsylvania, Indiana, Wisconsin and Massachusetts are shown in Figures 29-33.

The number of teeth in the serrations varies from three to nine, with the usual number being from six to eight.

The tip of valvula 2 exhibits some slight variations in form, but this is of little consequence. Some are slightly more blunt than the typical form; others are somewhat more narrowed.

DISTORTIONS

MALES

1. This specimen is in the collection of Iowa State University. Label data: (illegible word), New Mexico; 9,21,88. All parts of this insect are normal except the anterior arms of the styles which are half normal length and the anterior arm of the aedeagus which also is reduced. The aedeagus is illustrated in Figures 34 and 35.

2. The Iowa State University collection also contains this specimen. Label data: Boone, Iowa; 20 July, 1916; Collector L. S. Wells. This is again a normal-appearing insect in all respects except for the left style which is rather short and thick and has a dorso-lateral prominence; the upper part of the prominence is sclerotized and the lower part is membranous (Figs. 36 and 37).

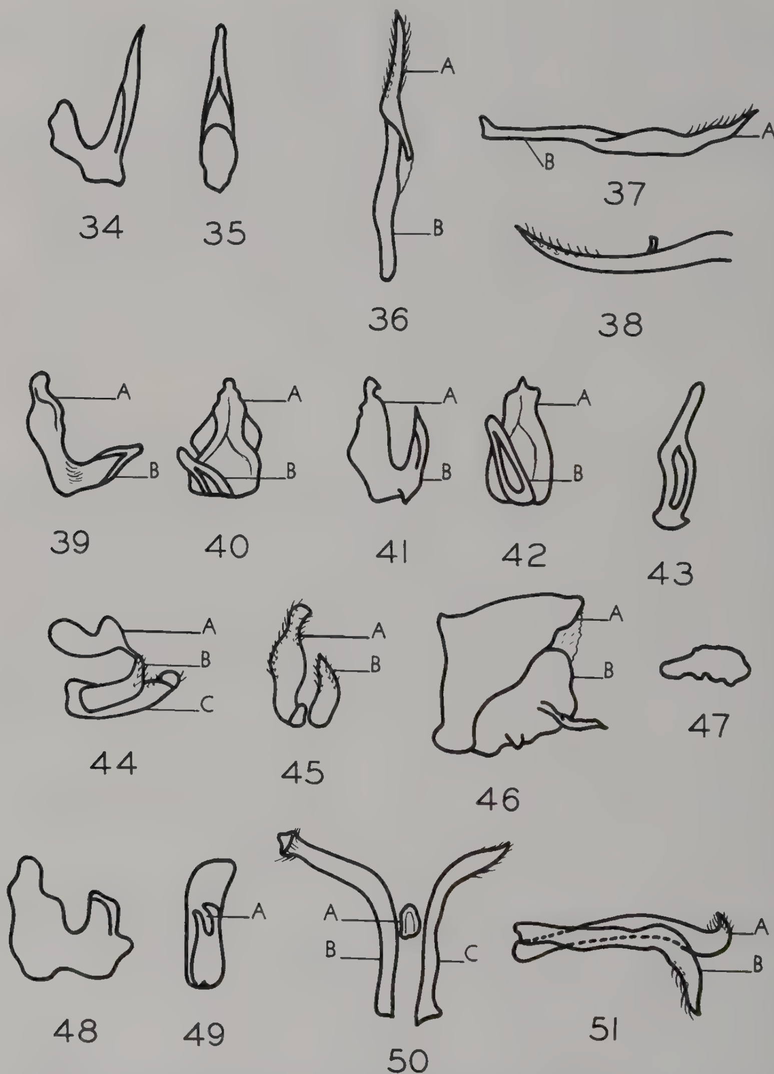
3. The Michigan State University collection contains this insect. Label data: Benton Harbor, Mich.; 2 Aug. 1939. The only distortion found is a slender dorsally directed spur at the basal one-third of the posterior arm of the right style (Fig. 38).

4. The collection of the University of Nebraska contains two specimens which are normal in appearance except for the aedeagus. The anterior arm is broadened and attached laterally to the posterior edges of the lateral valves; the posterior arm is somewhat distorted and tipped to the left.

Specimen "a" label data: Merriman, Nebraska; Cherry Co.; 7/31/32; Salix Fluv.; H. C. Jones; det Ceresa bubalus (Fabr.); H. C. Jones (Figs. 39 and 40). Specimen "b" label data: Baruston, Nebraska; (illegible word) Co.; 7/19/31; Black willow; A. A. Jones; Ceresa bubalus (Fabr.); det. H. C. Jones (Figs. 41 and 42).

5. This male is in the collection of the University of Wisconsin. Label data: Amery, Wisconsin; 9-14-17; E. D. Ball, Collector. This is a normal-appearing insect except for the subgenital plate, the aedeagus, the connective and the styles (Figs. 43-45).

The subgenital plate is slightly shorter than usual. The aedeagus appears nearly normal in lateral aspect, but when viewed in posterior



Figs. 34-51.—Male distortions. 34, 35. Aedeagus, specimen No. 1. 34. Left lateral. 35. Anterior. 36, 37. Left style, specimen No. 2. 36. Dorsal; A. Posterior arm; B. Anterior arm. 37. Lateral; A. Posterior arm; B. Anterior arm. 38. Posterior arm of right style, lateral, specimen No. 3. 39, 40. Aedeagus, specimen No. 4a. 39. Left lateral; A. Anterior arm; B. Posterior arm. 40. Posterior; A. Anterior arm; B. Posterior arm. 41, 42. Aedeagus, specimen No. 4b. 41. Left lateral; A. Anterior arm; B. Posterior arm. 42. Posterior; A. Anterior arm; B. Posterior arm. 43-45. Specimen No. 5. 43. Aedeagus, posterior. 44. Connective and styles, left lateral; A. Connective; B. Left style; C. Right style. 45. Styles,

aspect the posterior arm can be seen to be twisted. The connective is shortened and is joined by a thin bit of tissue to the apex of the left style. The right style is short, thick, curved inward at the tip and with only a tiny lobe to indicate the anterior arm. The left style is very short, upturned at the tip and has no indication of an anterior arm.

6. The University of Nebraska collection contains the most distorted male examined. Label data: Brownson, Nebraska; Cheyenne Co.; July 30, '32; rose; H. C. Jones; det. Ceresa bubalus (Fabr.); H. C. Jones. The terminalia of this specimen are distorted (Figs. 46-51).

Tergite IX has an irregular posterior margin and has membranous connections with the dorsal parts of the lateral valves. The lateral valves are irregular in shape; the left valve has a long, acute tooth above a short blunt tooth; the right valve lacks the long tooth. The subgenital plate is much reduced, being little more than a tiny, irregular scale.

Both arms of the aedeagus are rather short and thick. The lateral membranes of the posterior arm extend nearly to the top. The functional orifice is dorsal and extends a short distance down the posterior face. At its top, the posterior arm tips to the left. The connective is nearly normal but lacks the notch on the anterior margin. The anterior arms of the styles are short and thick; the posterior arms are strongly divergent at the tips. The posterior arm of the left style curves abruptly ventrally; the posterior arm of the right style has a dorsally recurved tip.

FEMALES

1. A specimen in the Michigan State University collection shows distortion of the tip of valvula 2 (Fig. 52). Label data: Benton Harbor, Mich.; 2 Aug. 1939; Ag. College; Lot 1562.

2. This specimen is in the collection of the Chicago Natural History Museum. Label data: Cook Co., Illinois; Col. and pres. by E. B. Chope. Except for the terminalia this is a normal-appearing female. The abdomen and genitalia are weakly sclerotized (Figs. 53-56).

Sternite VII is asymmetrical and has a broad, round-bottomed notch in its posterior margin. Valvulae 1 and valvula 2 are rather twisted-appearing. The left valvula 3 is absent; the right valvula 3 is only slightly distorted; the narrow anterior part is somewhat shorter than usual. The first valvifers are smaller than usual. The second valvifers are absent.

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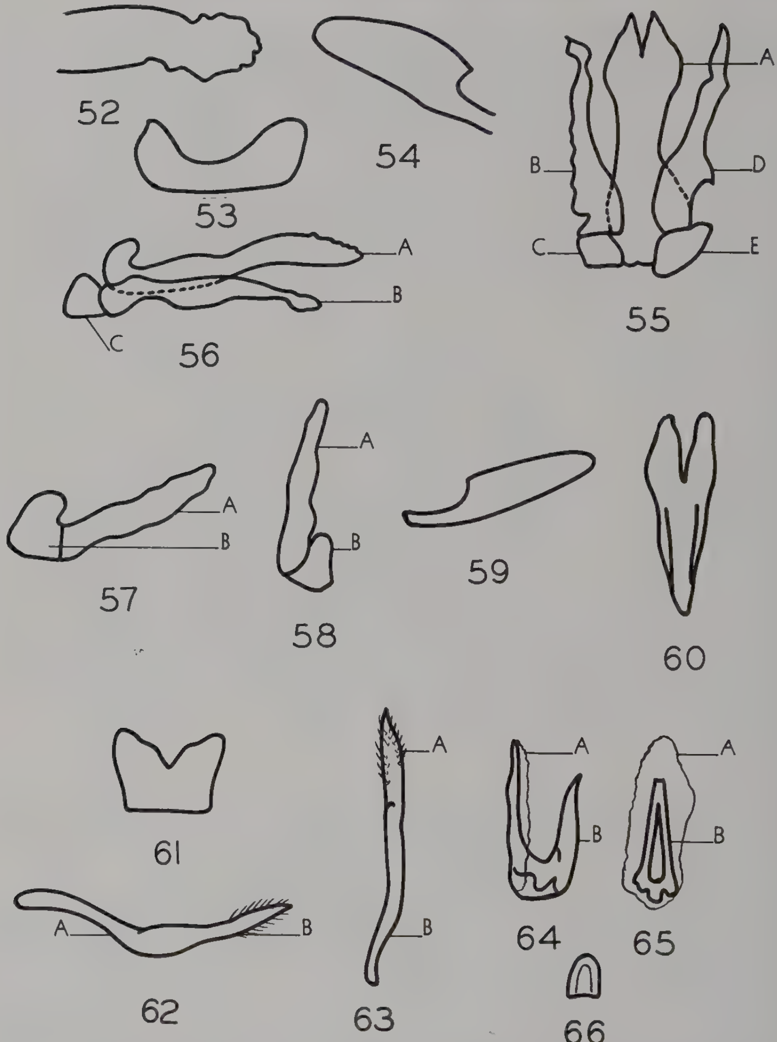
dorsal; A. Right style; B. Left style. 46-51. Specimen No. 6. 46. Tergite IX and left lateral valve, lateral; A. Tergite IX; B. Lateral valve. 47. Subgenital plate, ventral, posterior margin up. 48. Aedeagus left lateral. 49. Aedeagus, posterior; A. Functional orifice. 50. Styles and connective, dorsal; A. Connective; B. Right style; C. Left style. 51. Styles, left lateral; A. Right style; B. Left style.



Figs. 52-60.—Female distortions. 52. Valvula 2 tip, left lateral, specimen No. 1. 53-56. Specimen No. 2. 53. Sternite VII, ventral, posterior margin up. 54. Right valvula 3, lateral. 55. Valvulae 1, valvula 2, first valvifers, dorsal; A. Valvula 2; B. Right valvula 1; C. Right valvifer 1; D. Left valvula 1; E. Left valvifer 1. 56. Valvula 1, valvifer 1, valvula 2, left lateral; A. Valvula 2; B. Valvula 1; C. Valvifer 1. 57-60. Specimen No. 3. 57, 58. Left valvula 1 and left valvifer 1. 57. Lateral; A. Valvula 1; B. Valvifer 1. 58. Ventral; A. Valvula 1; B. Valvifer 1. 59. Right valvula 3, lateral. 60. Valvulae 3, ventral, posterior margin up. Figs. 61-66.—Both male and female parts present, specimen No. 1. 61. Sternite VII, ventral, posterior margin up. 62, 63. Left style. 62. Lateral; A. Anterior arm; B. Posterior arm. 63. Dorsal; A. Posterior arm; B. Anterior arm. 64, 65. Aedeagus. 64. Left lateral; A. Anterior arm; B. Posterior arm. 65. Posterior; A. Anterior arm; B. Posterior arm. 66. Connective, ventral, posterior margin up.

3. The female described here is in the collection of Ontario Agricultural College. Label data: Vineland, Ontario; Chas. A. Small; August 20, 1958. This specimen appears normal except for the genitalia which are distorted and about half normal size (Figs. 57-60).

The condyles near the base of tergite IX are fused in the midline. Sternite VII is of the normal shape but is small. Valvulae 1 have a short, thick form and are twisted-appearing. Valvula 2 is represented by remnants. Valvulae 3 are ventrally fused at the midline in the basal two-thirds; the narrow basal parts of these valvulae are rather short. The first valvifers are nearly normal. The second valvifers are absent.

WITH BOTH MALE AND FEMALE PARTS

1. This specimen is in the collection of Cornell University. Label data: Babylon, L.I., N.Y.; 8-3-1933; F. S. Blanton; Ceresa bubalis Fabr.; det. P. W. Oman. This seems to be essentially a distorted male, but it has a sternite VII like a female. There is no other evidence of female parts. Except for the genitalia it appears to be a normal specimen (Figs. 61-66).

The subgenital plate lacks its left tip. But this appears to have been broken or chewed off. The anterior arm of the aedeagus is slender in lateral aspect and somewhat broadened by membranous tissue; the posterior arm is irregular below and with the lateral membranes well below the middle. The ventral lobe of the aedeagus is missing. The connective lacks the anterior notch. The styles are somewhat thickened in the middle and in the posterior arms.

2. The specimen described here could be called a pseudohermaphrodite. It is in the collection of the University of Massachusetts. Label data: Ceresa bubalus; det. E. C. Lerch; 1572. There is no locality information given; but, according to information received from Professor Shaw, it was probably collected near Amherst, Massachusetts.

The specimen appears to be a normal, though slightly small-sized female. The abdomen and genitalia are weakly sclerotized; genitalia are slightly reduced in size (Figs. 67-73). The female parts enclose the male parts.

Female parts.—Tergite IX and the anal tube are normal. Sternite VII is slightly asymmetrical and has a shallowly notched posterior margin.

Valvulae 1 are somewhat twisted in appearance. Valvula 2 is separated into right and left parts. In lateral aspect the appearance of this valvula is only slightly distorted. However, when seen in ventral aspect, valvulae 2 are crescent-shaped. Valvulae 3 are nearly normal.

The first valvifers are asymmetrical and fused ventrally. The second valvifers are somewhat larger than usual.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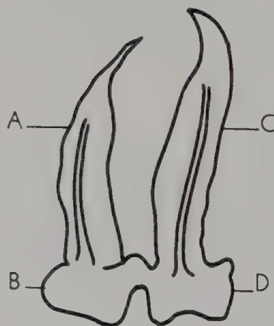

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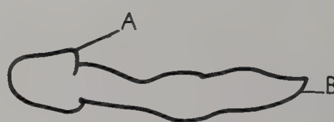

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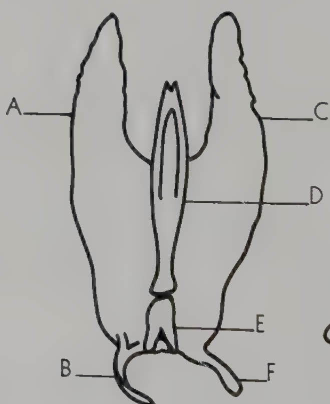

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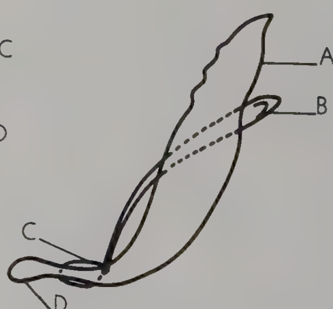

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Figs. 67-73.—Both male and female parts present, specimen No. 2. 67-71. Female parts. 67. Sternite VII, ventral, posterior margin up. 68. Valvulae 2, 3, valvifer 2, left lateral; A. Valvula 3; B. Valvifer 2; C. Valvula 2. 69. Left valvula 2, ventral. 70. Valvulae 1 and first valvifers, ventral; A. Left valvula 1; B. Left valvifer 1; C. Right valvula 1; D Right valvifer 1. 71. Left valvula 1

Male parts.—The lateral valves and the subgenital plate are missing.

The anterior arm of the aedeagus is absent. The posterior arm is rather slender in lateral aspect; especially toward the base. In anterior aspect this posterior arm can be seen to be slightly broadened at the base, acutely notched at the tip and with the functional orifice incomplete below. The base of the aedeagus articulates with the posterior edge of the connective.

The connective has the notch on the anterior margin deeper than usual and is enclosed in the membranous bases of the posterior arms of the styles.

The anterior arms of the styles are very short; the posterior arms are long and broad and basally fused along their ventral margins for half of their length. The basal parts of the posterior arms are membranous; the distal parts are more heavily sclerotized. Each posterior arm is dorsally coarsely serrate before the tip, presenting an appearance similar to that of valvula 2 of the female.

3. The collection of North Carolina State College contains another pseudohermaphrodite. Label data: Syracuse, N.Y.; 5/22/18; A. J. Basinger, Collector. This specimen otherwise appears to be a normal full-sized female. The genital parts are about two-thirds normal size (Figs. 74-80). The female parts enclose the male parts.

Female parts.—Tergite IX and the anal tube are normal. Sternite VII is asymmetrical; its posterior margin is a broad, obtuse notch.

Valvulae 1 are crescent-shaped with a ventral curvature when seen laterally. They are nearly straight in ventral aspect. Valvula 2 is separated into right and left parts. Laterally, they appear twisted and shortened and lack the coarse dorsal serrations before the tip. When viewed in ventral aspect valvulae 2 are crescent-shaped. Valvulae 3 are normal.

The first valvifers are slightly distorted. The second valvifers are shorter and thicker than usual.

Male parts.—The lateral valves and the subgenital plate are lacking.

The anterior arm of the aedeagus is absent. The posterior arm consists of about the upper two-thirds of a normal posterior arm; the base of the posterior arm is about halfway up the styles.

The connective is irregular in shape. It is positioned at the base of the posterior arm of the aedeagus. The base of the aedeagus and the connective are suspended in a hood-like membrane which originates laterally on the styles.

The anterior arms of the styles are convergent and upturned; the

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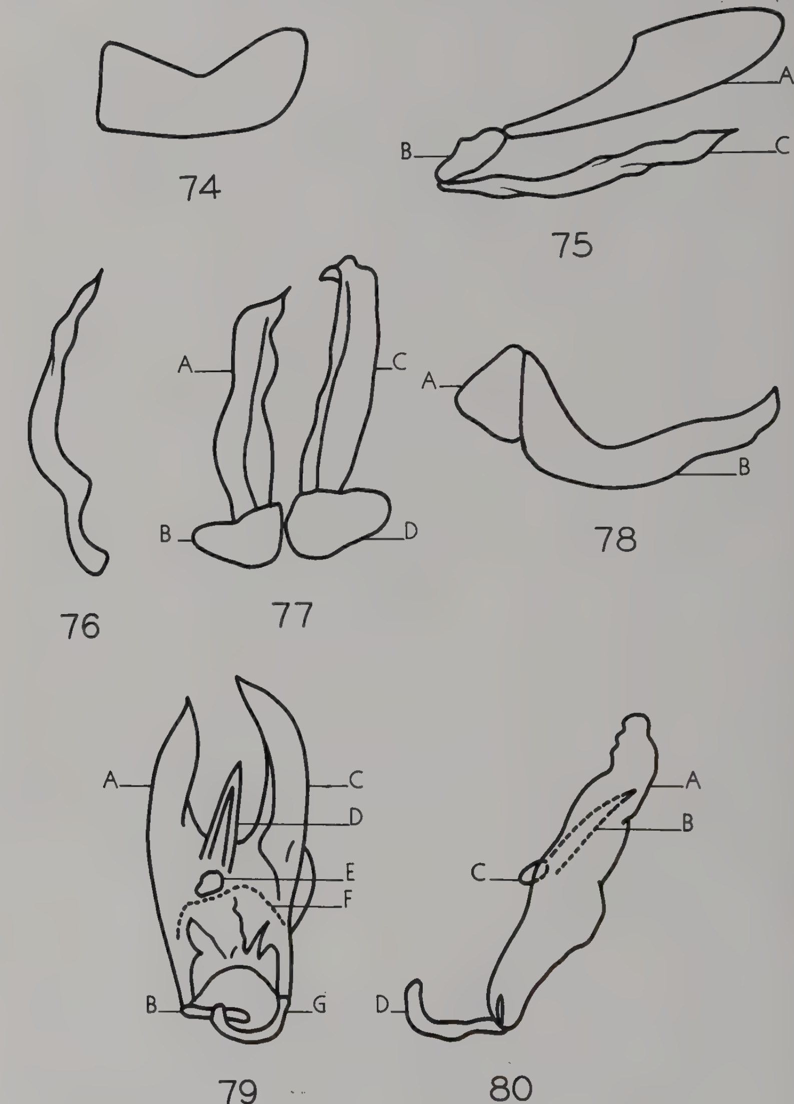
and first valvifer, lateral; A. Valvifer 1; B. Valvula 1. 72, 73. Male parts. 72. Anterior; A. Right style, posterior arm; B. Right style, anterior arm; C. Left style, posterior arm; D. Aedeagus; E. Connective; F. Left style, anterior arm. 73. Left lateral A. Left style, posterior arm; B. Aedeagus; C. Connective; D. Left style, anterior arm.



Figs. 74-80.—Both male and female parts present, specimen No. 3. 74-78. Female parts. 74. Sternite VII, ventral, posterior margin up. 75. Valvulae 2, 3, valvifer 2, left lateral; A. Valvula 3; B. Valvifer 2; C. Valvula 2. 76. Left valvula 2, ventral. 77. Valvulae 1 and first valvifers, ventral; A. Left valvula 1; B. Left valvifer 1; C. Right valvula 1; D. Right valvifer 1. 78. Left valvula 1 and first valvifer, lateral; A. Valvifer 1; B. Valvula 1. 79, 80. Male parts. 79. Anterior; A. Right style, posterior arm; B. Right style, anterior arm; C. Left style, posterior arm; D. Aedeagus; E. Connective; F. Membrane; G. Left style, anterior arm. 80. Left lateral; A. Left style, posterior arm; B. Aedeagus; C. Connective; D. Left style, anterior arm.

posterior arms are long and broad and basally fused along their ventral margins for slightly over half of their lengths. The basal, central areas of the styles are weakly sclerotized; the remainder is more strongly sclerotized. Each posterior arm has obscure, coarse dorsal serrations before the tip, presenting an appearance similar to that of the female valvula 2.

DISCUSSION

In the male, abdominal tergites IX, X and XI, the lateral valves, the subgenital plate and the connective are rather constant. The teeth of the lateral valves, the styles, the posterior arm and the ventral lobe of the aedeagus have minor variations. The anterior arm of the aedeagus is highly variable.

In the female, abdominal tergites IX, X and XI, abdominal sternite VII, valvifers 1 and 2 and valvulae 1 and 3 are rather constant. Valvula 2 exhibits some variations in the form of dorsal teeth and serrations before the tip.

Only thirteen specimens exhibit any particular distortion, and in four of these the distortion is minor. Reasons for these distortions are unknown. Kornhauser (1919) reported distortion and weak sclerotization of the abdomen and genitalia of the treehopper *Thelia bimaculata* (Fabricius) due to parasitism. In earlier work I found parasites and similar distortions in a few specimens of the treehoppers *Ophiderma salamandra* Fairmaire, *Archasia belfragei* Stal, *Palonica tremulata* (Ball), *Telamona monticola* (Fabricius), *T. tiliae* Ball and *T. spreta* Goding, but no parasites were found in any of the distorted specimens examined during this study.

Except for the anterior arm of the aedeagus and a few variations in valvula 2, the uniformity of the genitalia of the specimens is striking.

Caldwell's (1949) revision of the Ceresini is a step in the right direction. However, it is suggested that the females be considered as well as the males and that a long series of specimens of each species be studied to establish as accurately as possible the amount of variation and uniqueness of genital parts.

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Physicochemical Properties and Differentiation of Chromatophorotropins and Retinal Pigment Light-Adapting Hormone of the Dwarf Crayfish, *Cambarellus shufeldti*[1]

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Recent investigations conducted with the crayfishes *Cambarellus shufeldti* and *Orconectes clypeatus* have been directed toward explaining regulation of pigment migration in the chromatophores and retinal pigment cells (Fingerman, 1957a, b, 1958; Fingerman and Aoto, 1958; Fingerman and Lowe, 1957, 1958; Fingerman, Mobberly, and Sundararaj, 1959). Evidence from these studies supports the hypothesis that the dark red chromatophoral pigment in both species is controlled by dispersing and concentrating substances while the distal retinal pigment is regulated by light-adapting and dark-adapting hormones. Little, however, is known of any relation between chromatophorotropins and retinal pigment activators, *e.g.*, whether these are identical or different substances.

Edman, Fänge, and Östlund (1958), in attempting to isolate red pigment-concentrating hormone from eyestalks of *Pandalus borealis,* reported that the hormone was electronegative at pH 2.5, 4.0, 7.0, and 9.0. They were unable to reverse its charge or to get a positive reaction in the Reindel and Hoppe test for peptides. The hypothesis that neurosecretory products of crustaceans are polypeptides was proposed by Knowles and Carlisle (1956) and is based on physicochemical properties studied by them.

The present investigation was undertaken using *Cambarellus* to determine the electrophoretic behavior of chromatophorotropins at different pH values and to learn whether the retinal pigment light-adapting hormone is identical with or different from the chromatophorotropins in the eyestalk.

Materials and Methods

Specimens of the dwarf crayfish, *Cambarellus shufeldti,* were collected in roadside ditches at Hickory, Louisiana, for use in the experiments described below. The crayfish were kept in aquaria that contained dechlorinated tap water approximately one inch deep.

Extracts of tissues known to contain hormonal substances were assayed on dwarf crayfish from which one eyestalk had been removed at least 12 hours prior to experimental use. Brown, Webb, and Sandeen (1952) and Fingerman (1957a) found that one-eyed individuals were more sensitive to chromatophorotropins than intact specimens.

[1] This investigation was supported by Grant No. B-838 from the National Institutes of Health.

For this reason one-eyed animals were also used in assays for distal retinal pigment light-adapting hormone.

The effect of an extract on body coloration was determined by recording the stages (Hogben and Slome, 1931) of the integumentary dark red chromatophores that lie dorsal to the heart. Stage 1 represents maximal concentration of pigment, stage 5 maximal dispersion, stages 2, 3, and 4 the intermediate conditions. The exoskeleton of *Cambarellus* is sufficiently transparent to allow direct, accurate observation of the underlying chromatophores.

The method of Sandeen and Brown (1952), as modified by Fingerman (1957b) for use with crayfishes, was employed to determine the effect of an extract on the distal retinal pigment of *Cambarellus*. This method entails the following procedure. With the aid of an ocular micrometer and a stereoscopic dissecting microscope the following measurements were made by transmitted light: (1) the width of the translucent distal portion of the eye in a plane parallel to the long axis of the eyestalk and (2) the length of the eye from the corneal surface to the apex of the notch at the proximal portion of the eye. The ratio of length of clear area (measurement 1) to total length (measurement 2) is known as the distal pigment index. Use of this ratio minimizes effects of size differences. The distal pigment index of 10 crayfish can be determined with ease in three minutes.

Potency values were used to facilitate comparison of the effects of different extracts. Values for chromatophorotropins were calculated as described by Sandeen (1950). The stage of the dark red chromatophores of each crayfish receiving chromatophorotropins or control saline (Van Harreveld, 1936) was recorded at the time of injection and 15, 30, 60, 90, and 120 minutes thereafter. The mean chromatophore stage at the start of every experiment was 1.0; the crayfish were in white pans. The six average chromatophore stages for each group of crayfish were summed. Six was then subtracted from the sum because if no dispersion of red pigment had occurred the sum would have been six. Finally, the value of the control group was subtracted from the value obtained from crayfish injected with hormone.

Potency values for extracts containing distal retinal pigment light-adapting hormone were calculated similarly. The mean distal pigment indices recorded 30, 60, 90, and 120 minutes after the extracts and saline had been injected were summed. The sum for the control group was subtracted from the sum of the experimental group and the difference was the potency value. These values have the advantage of taking into account both amplitude and duration of response.

Filter paper electrophoresis was performed in the manner described earlier by Fingerman and Lowe (1957) and Fingerman and Aoto (1958). A model E-800-2 Filter Paper Electrophoresis Apparatus manufactured by the Research Equipment Corporation was used. The voltage was 500 volts and the current 0.1 milliampere. In the preparation of extracts the excised tissues were triturated in 0.1 ml distilled water. Each extract contained either 40 eyestalks or 20 supraesopha-

geal ganglia with the circumesophageal connectives attached. Extracts of eyestalks were centrifuged to remove the bits of exoskeleton and retinal pigments.

The supernatant was applied in aliquots to a 0.5-inch-wide strip of Whatman No. 1 filter paper. A cool-air blower was used to dry the strip after each application; the entire supernatant was thus contained in a band not more than one-quarter inch wide. The strip of

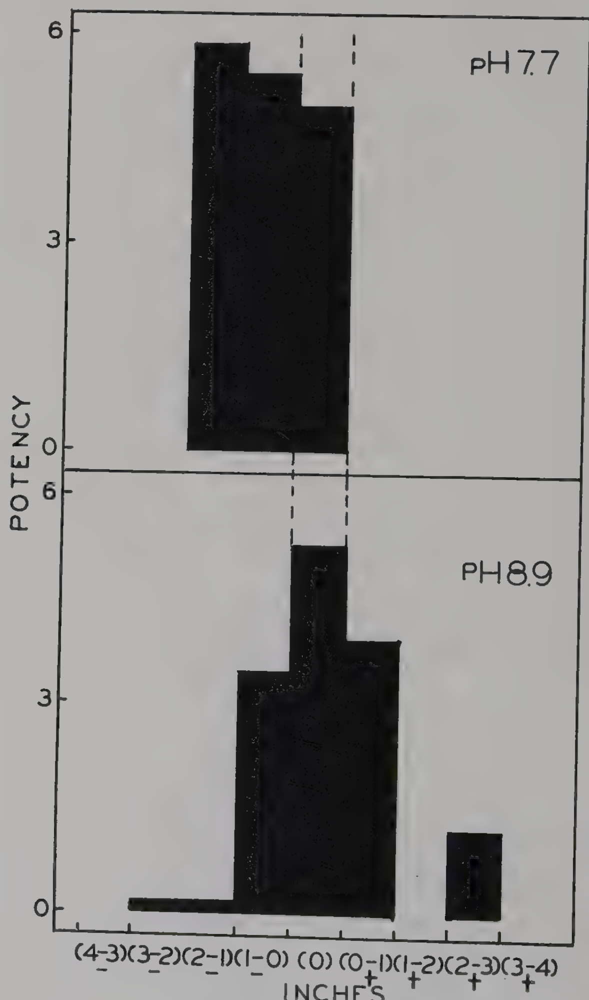

Fig. 1.—Red pigment-dispersing potencies of extracts of eyestalks of *Cambarellus* versus position on the filter paper strip after electrophoresis at pH 7.7 and 8.9.

filter paper was then moistened with the appropriate buffer and placed in the electrophoresis migration chamber. The buffers used were 0.1M sodium hydroxide-boric acid for pH values from 7.7 to 9.0 and a mixture of 0.05M citric acid and 0.1M dibasic sodium phosphate of pH 2.3. To minimize the inactivation of chromatophorotropins that occurs when extracts are kept at room temperature (Fingerman and Lowe, 1957) the chamber was kept in a refrigerator maintained at an average temperature of 7°C. After electrophoresis had proceeded for two hours the filter paper strip was removed from the chamber and cut into segments. The number and length of the segments depended upon the experiment. The sections of the strip were placed immediately into 0.3 ml Van Harreveld's solution in covered containers and then kept in the refrigerator for 30 minutes to allow materials to wash from the paper. The fluid was then collected in syringes and 0.02 ml injected into each test animal. Control extracts were prepared by similar elution of segments of buffer-moistened filter paper with 0.3 ml Van Harreveld's solution for 30 minutes.

EXPERIMENTS AND RESULTS

Electrophoretic behavior of chromatophorotropins

The objective of this set of experiments was to determine the direction and distance of migration of chromatophorotropins of *Cambarellus* when filter paper electrophoresis was performed at different pH values. Analyses were performed in the manner described under Materials and Methods.

Extracts of eyestalks were subjected to electrophoresis at pH 7.7 and pH 8.9. The experiment at each pH was performed three times and the results of the corresponding experiments were qualitatively alike. The data obtained at each pH were averaged and the mean potency values were used in the preparation of Figure 1. Inspection of this figure reveals that at pH 7.7 the red pigment-dispersing hormone was electropositive, consequently migration was toward the cathode. At pH 8.9, however, migration occurred toward both poles, but more material remained at the origin than was found in any of the assayed sections of the filter paper strip on either side of the origin. The behavior at pH 8.9 must have been due to reversal of the charge on at least some of the molecules of red pigment-dispersing hormone from the eyestalk. The isoelectric point of this hormone is probably close to pH 8.9.

The next substance investigated was the red pigment-dispersing hormone found in the supraesophageal ganglia and circumesophageal connectives. Fingerman and Aoto (1958) have already shown that the red pigment-dispersing hormone in the supraesophageal ganglia and circumesophageal connectives cannot be the same substance as the red pigment-dispersing hormone found in the eyestalk. One point of evidence was the fact that at pH 7.5 the material in the eyestalk was electropositive as was the case at pH 7.7 (Fig. 1), whereas

the hormone in the supraesophageal ganglia and circumesophageal connectives was electronegative at pH 7.5.

In the present investigation the red pigment-dispersing hormone in the supraesophageal ganglia and circumesophageal connectives was subjected to electrophoresis at pH 2.3 and pH 7.7 (Fig. 2). The experiment at each pH was done three times. At the acid pH the hormone was electropositive, whereas at the higher pH the substance was electronegative. Presumably, its isoelectric point is around pH 5.0.

Comparison of the electrophoretic behavior of chromatophorotropins and distal retinal pigment light-adapting hormone

The objective of this set of experiments was to demonstrate that the distal retinal pigment light-adapting hormone is not identical with any of the chromatophorotropins in the eyestalk of *Cambarellus*. The light-adapting and red pigment-dispersing hormones occur in greater quantity than their antagonists in the eyestalks of *Cambarellus* (Fingerman, 1957a; Fingerman, Mobberly, and Sundararaj, 1959). If these hormones do not have the same electrophoretic behavior, then one would be justified in concluding that they are not identical substances.

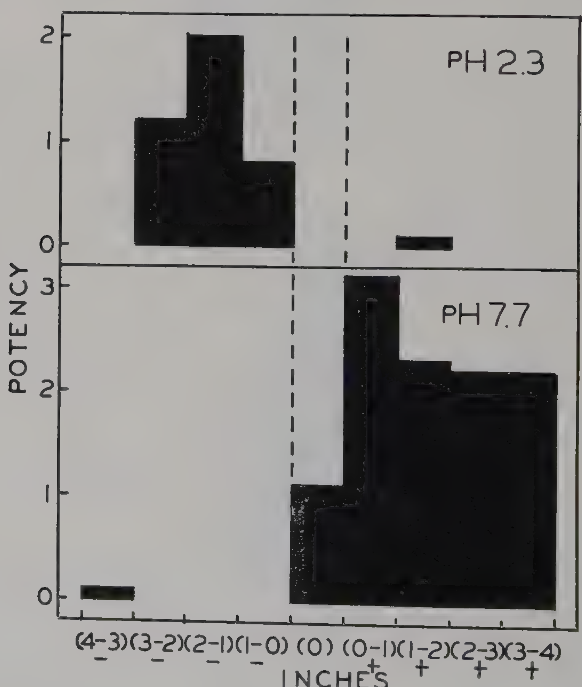

Fig. 2.—Red pigment-dispersing potencies of extracts of supraesophageal ganglia with the circumesophageal connectives attached of *Cambarellus* versus position on the filter paper strip after electrophoresis at pH 2.3 and 7.7.

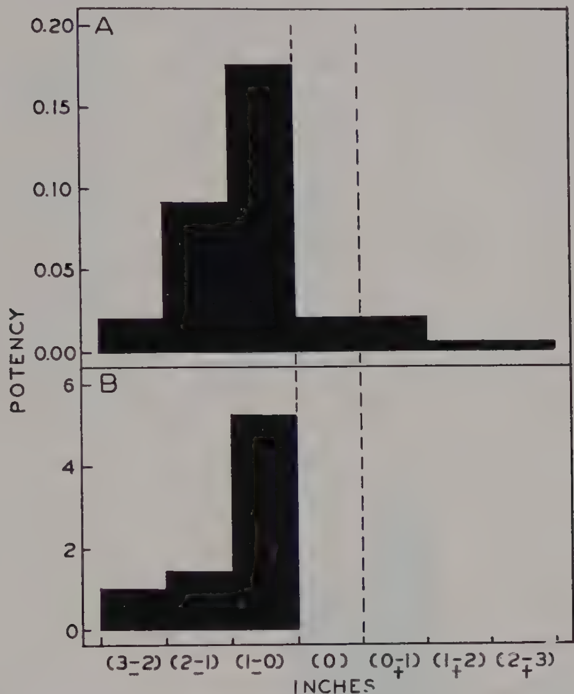

Fig. 3.—Comparison of (A) distal retinal pigment light-adapting potencies and (B) red pigment-dispersing potencies of eyestalk extracts of dwarf crayfish subjected to filter paper electrophoresis at pH 7.8 for two hours.

In the first experiment of this group the pH used was 7.8. One-inch portions on the anodal and cathodal sides of the origin were used in the assay. The extract from each section of the strip was assayed on dwarf crayfish in (1) a white container to determine the red pigment-dispersing potency and (2) a black pan under an illumination of 29 ft.c. to determine the distal retinal pigment light-adapting potency. At this light intensity the distal pigment was in a position approximately midway between the fully light-adapted and dark-adapted positions (Fingerman, Mobberly, and Sundararaj, 1959).

The results of this experiment are shown in Figure 3. The figure shows that the first inch on the cathodal side of the origin contained more light-adapting and red pigment-dispersing hormone than any other section of the strip. The small amounts of light-adapting activity at the origin and on the anodal side were probably not significant. From this figure alone one could not conclude that these substances are different. Since this light-adapting hormone is electropositive at pH 7.8, it could not be identical with the red pigment-concentrating

hormone of the eyestalk which is electronegative at even the slightly lower pH of 7.5 (Fingerman and Aoto, 1958).

The next experiment was designed to separate at least partially the red pigment-dispersing hormone from the distal retinal pigment light-adapting substance by taking advantage of the fact that some of this chromatophorotropin migrates toward the anode at high pH values as shown in Figure 1. This experiment was performed at pH 9.0 four times. No qualitative difference was observed among the results of the four experiments. Consequently, the data were averaged and the means are presented in Figure 4. In each instance an appreciable amount of the chromatophorotropin migrated toward the anode whereas very little light-adaptation was produced by the extracts from the anodal side of the strip. These results support the hypothesis that the two substances are different from each other.

To determine the percentage of the original quantity of each hormone that was recovered from the filter paper strips the following

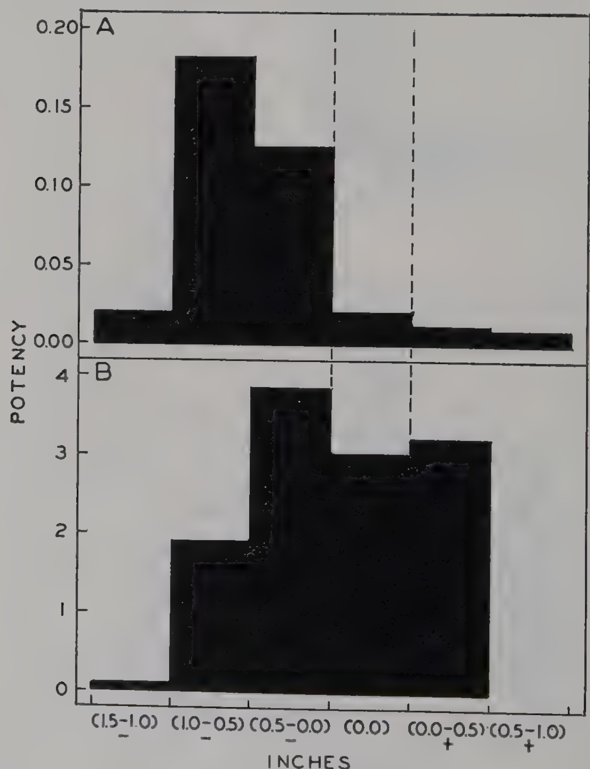

Fig. 4.—Comparison of (A) distal retinal pigment light-adapting potencies and (B) red pigment-dispersing potencies of eyestalk extracts of dwarf crayfish subjected to filter paper electrophoresis at pH 9.0 for two hours.

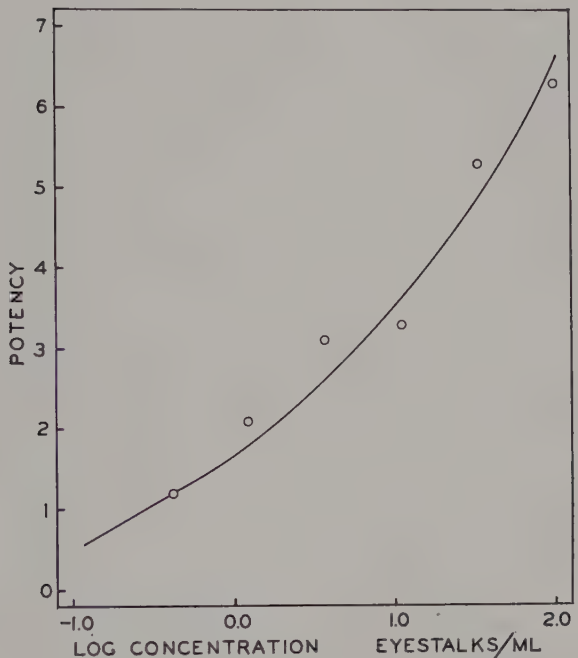

Fig. 5.—Relationship between red pigment-dispersing potency and the logarithm of the concentration of eyestalks of dwarf crayfish.

procedure was employed. Extracts of eyestalks were prepared in six concentrations, 1/243, 1/81, 1/27, 1/9, 1/3 and 1 eyestalk per 0.01 ml Van Harreveld's solution, and injected into dwarf crayfish with maximally concentrated dark red pigment to determine the red pigment-dispersing potency and into *Cambarellus* in black pans under an illumination of 29 ft.c. to obtain the light-adapting potency. Control animals were injected with Van Harreveld's solution. The experiment was performed three times. The concentration in eyestalks/ml that corresponded to the mean potency value obtained with each section of the filter paper strips depicted in Figures 3 and 4 was then read from the corresponding dosage-response curve (Fig. 5 or 6). The potencies of all the sections of each strip were summed and the sum was multiplied by 0.3 because 0.3 ml rather than 1.0 ml of Van Harreveld's solution was used to elute the hormones from each section of the strip. The product was the number of eyestalks equivalent to the amount of hormone recovered from the strip. The values for Figures 3A, 3B, 4A, and 4B were 20.2 eyestalks (50.8% recovery), 12.3 eyestalks (30.3%), 24.8 eyestalks (61.5%), 7.5 eyestalks (18.8%) respectively. The recovery of light-adapting hormone was greater than the recovery of chromatophorotropin (50.8% and 61.5% versus 30.3%

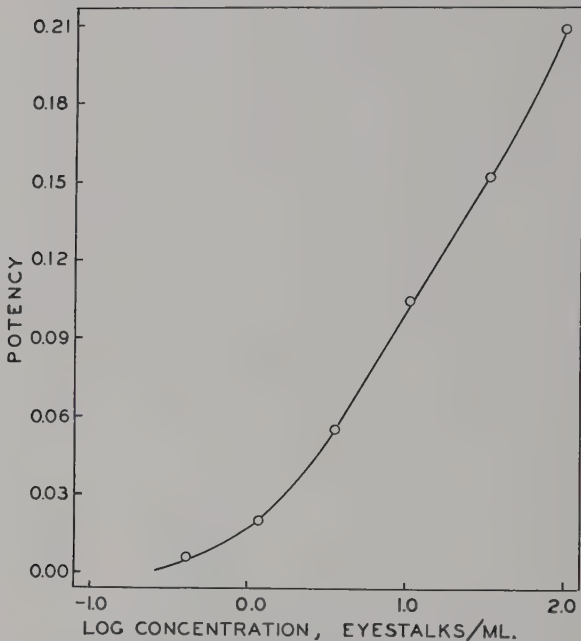

Fig. 6.—Relationship between light-adapting potency and the logarithm of the concentration of eyestalks of dwarf crayfish.

and 18.8%). Two possible explanations of this difference are (1) the chromatophorotropin may be absorbed to filter paper more firmly than the retinal pigment activator and (2) the chromatophorotropin may decay faster than the light-adapting hormone.

Discussion

Edman, Fänge, and Östlund (1958) reported that the charge on the red pigment-concentrating hormone of *Pandalus* did not reverse when electrophoresis was performed at pH 2.5, 4.0, 7.0, and 9.0. Red pigment-dispersing hormone in the eyestalk of *Cambarellus* was electropositive at pH 7.7 (Fig. 1) but pH 8.9 appeared to be close to its isoelectric point. Some of the molecules had become electronegative. The results at pH 7.7 (Figs. 1 and 2) were in agreement with those reported earlier at pH 7.5.

The fact that the red pigment-dispersing hormone in the eyestalk is electropositive at pH 7.7, whereas, its functional counterpart in the supraesophageal ganglia and circumesophageal connectives is electronegative at this pH is open to two possible explanations: (1) the two hormones are completely different substances or (2) the same active unit could be attached to either of two proteins. The latter possibility

occurs with thyroxine (Ingbar, 1958). Thyroxine is normally bound to alpha globulin, but may be bound to pre-albumen. Fingerman and Aoto (1958) discussed the question of why one animal would synthesize two substances with the same function. The red pigment-dispersing hormone of the eyestalk reaches its maximum effectiveness more rapidly than does the red pigment-dispersing hormone from the supraesophageal ganglia and circumesophageal connectives (Fingerman, 1957a). The substance from the eyestalk may be used to move the pigment rapidly to the desired degree of dispersion, and once this stage has been attained the hormone from the supraesophageal ganglia and circumesophageal connectives may take over to maintain the condition.

The sensitivity of chromatophorotropins to trypsin and chymotrypsin has been reported by several investigators (*e.g.*, Pérez-González, 1957; Edman, Fänge, and Östlund, 1958) and has been interpreted as evidence in favor of the concept that neurosecretory products in crustaceans are polypeptides. Chromatophorotropins of *Cambarellus* are also inactivated by trypsin (unpublished data). These enzymes, however, also have some esterase activity so that trypsin sensitivity alone is not absolute evidence for a polypeptide. Charge reversal as shown in Figures 1 and 2, however, provides strong evidence for a polypeptide structure rather than an ester one.

Geschwind (1959) discussed the species variation in protein and polypeptide hormones. Two types (α and β) of melanophore stimulating hormone (MSH) have been found in the intermediate lobe of pig and ox pituitaries. The α-form of MSH is a very basic peptide with an isoelectric point between 10.5 and 11.0. Porcine β-MSH is acidic with an isoelectric point of 5.8 and bovine β-MSH has an isoelectric point of 7.0. The substitution of a single amino acid in the molecule accounts for the difference between the isoelectric points of porcine and bovine β-MSH. The occurrence of two forms of MSH in the same pituitary may be analogous to that observed with the red pigment-dispersing hormones in *Cambarellus*. Ultimate determination of the chemical structure of chromatophorotropins in crustaceans may show further similarities between them and α- and β-MSH.

The authors take pleasure in thanking Dr. L. H. Kleinholz for his helpful suggestions in the preparation of this manuscript. The responsibility for any errors and for the conclusions, however, is entirely our own.

Summary and Conclusions

1. The red pigment-dispersing hormone in the eyestalk of *Cambarellus* is electropositive at pH 7.7. Its isoelectric point is near pH 8.9.

2. The red pigment-dispersing hormone in the supraesophageal ganglia and circumesophageal connectives is electropositive at pH 2.3, but electronegative at pH 7.7. Its isoelectric point is probably near pH 5.0.

3. The distal retinal pigment light-adapting hormone in the eye-

stalks of *Cambarellus* is not identical with either of the chromatophorotropins found in the eyestalks.

4. The data support the hypothesis that neurosecretory products of crustaceans are polypeptides.

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Variations Among the Spores of the Microsporidian Perezia pyraustae Paillot

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Introduction

In a previous paper the author (Kramer, 1959) reported the results of a study on the developmental cycle of the microsporidian *Perezia pyraustae* Paillot, an important parasite in the natural control of the European corn borer, *Pyrausta nubilalis* (Hübner) (Kramer, 1959a and 1959b). Among the various stages in the development of *P. pyraustae* and other microsporidians, the spore is of prime importance since it is the infective form of the parasite which is most often transmitted from one host to another. Notable differences are to be found among the spores of *P. pyraustae* recovered from any spore-laden host tissue. The present paper concerns these differences and their probable significance.

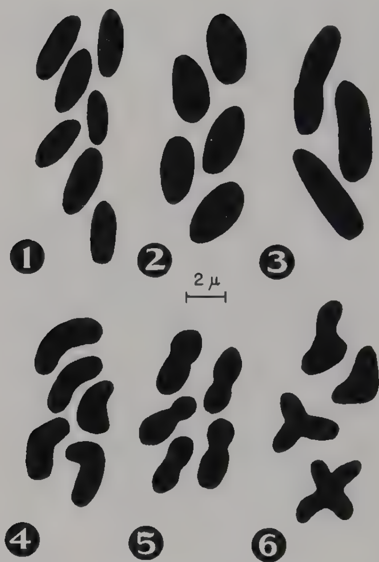
Materials and Methods

At irregular intervals over the past five years the author has examined several thousand larval, pupal, and imaginal *P. pyraustae*-infected *P. nubilalis* collected in Illinois. Among the tens of thousands of *P. pyraustae* spores recovered from feces, haemolymph, fat bodies, silk glands, malpighian tubes, gonads, and ventriculi, several different forms have been observed and are shown in Figures 1-6. While these sketches are based upon spores observed in fixed and stained smears of spore-laden host tissues, similar forms were observed in suspensions of fresh spores in invertebrate saline solution. Smears were briefly air-dried, fixed in a 2 per cent aqueous solution of osmium tetroxide for four to six hours, and stained with Giemsa stain for twelve to thirty-six hours. The nomenclature applied to the various forms of the spore is taken in part from the monumental work of Kudo (1924).

Observations and Discussion

In practically all spore-laden host tissues, irrespective of their origin, all types of spores are to be found in varying proportions. A vast majority of the spores are ovocylindrical to ovoidal in form (Figs. 1-2). Not uncommon are the reniform and didymiform types (Figs. 4-5). Rarely one sees the tubular forms (Fig. 3) and the irregular types (Fig. 6). Yet on occasion the author has encountered presumably pure cultures of the ovocylindrical type. Less frequently the author has observed masses of spores which appear to be entirely of the ovoidal type.

Information relating to the significance of these apparent differ-



Figs. 1-6.—Variations in the spores of the microsporidian *Perezia pyraustae* Paillot. 1. Ovocylindrical. 2. Ovoidal. 3. Tubular. 4. Reniform. 5. Didymiform. 6. Irregular.

ences was obtained by measuring several hundred spores selected at random from apparently pure cultures of both the ovocylindrical and ovoidal types. The measuring device was a Leitz OKNOR screw micrometer eyepiece which affords greater accuracy than the standard micrometer scale eyepiece. The length of ovocylindrical spores varied from 2.29 to 3.99 μ while the length of ovoidal spores ranged from 2.90 to 4.60 μ. The width of ovocylindrical spores ranged from 1.06 to 1.84 μ while the width of ovoidal spores varied from 1.13 to 2.35 μ. Although the length and width of spores varied somewhat independently, an obvious overlap exists between these two spore types. It must be pointed out that the measurements given above are to some extent different from those reported earlier (Kramer, 1959). Doubtless the present measurements are more nearly accurate since they were made with the aforementioned Leitz OKNOR which eliminates to a considerable degree the problem of estimation inherent in the use of the standard micrometer eyepiece which was employed in the earlier study.

The tubular and irregular forms are probably anomalies which result from the absence of cytoplasmic division of sister cells during sporogony. The shape of the reniform and didymiform types probably has been influenced by overcrowding of the parasite population within host cells. The didymiform types in all likelihood result from incomplete separation of sister sporoblasts. It should be noted that the aforementioned reniform and didymiform spores are fairly comparable to the curved and double spores noticed by Hall (1952) in his study of *P. pyraustae* as a parasite in the buckeye caterpillar, *Junonia coenia* Hübner. Of additional interest here is the rather

common occurrence of reniform spores in populations of *P. fumiferanae* Thomson, a parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Thomson, 1959).

The variations observed in the present study pertaining to the ovocylindrical and ovoidal spore types might lead one to suppose that more than one species of microsporidian is present, perhaps even representing two or more genera. This is unlikely since the only recognizable sporonts associated with the spores in question were disporous. This clearly indicates that only the genus *Perezia* is involved. A clue to the real significance of these variations in dimensions lies in the fact that intermediates can be found within any aggregation of microsporidian spores recovered from *P. nubilalis*. Walters (1958) has amply demonstrated a similar type of variation among the spores of a *Nosema* species originally isolated from the cecropia moth, *Hyalophora cercropia* (Linneaus). These variations in dimensions and the anomalous variations in form (discussed in the preceding paragraph) reflect the sort of differences one might expect in any large population of a single species of Microsporidia or, for that matter, any animal. The obvious conclusion is that until the taxonomic characters used in separating the Microsporidia are more clearly defined, particularly at the species level (see Poisson, 1953), extreme caution should be exercised in the creation of new species based solely upon the dimensions and shape of spores.

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Litter Size and Latitude in North American Mammals

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The phenomenon of fluctuations of mammal populations in the higher latitudes of the northern hemisphere is well known. Clearly, population changes of such magnitudes are evidence that large mortality rates are being experienced by these species. Because such large fluctuations in populations seldom occur in the lower latitudes, it seems apparent that species in these latitudes may not often experience the large mortality rates of closely allied species to the north.

The principle of inversity as expressed by Errington (1946) and others, seems to imply that the species of the high latitudes experiencing the high mortality rates will have correspondingly high reproductive rates to help compensate for their losses. Because the breeding season in the north is shorter than that in more southern latitudes, there is less opportunity for increasing reproduction by way of more litters during the season than there is by an increase in the litter size. Therefore, the average litter size of mammals of the same or closely related species should increase with an increase in latitude. Rowan and Keith (1956) for the snowshoe hare and Burns and Burns (1957) for the opossum have shown that such an increase does occur. Moore (in press) has also shown the effect of climate on reproduction in the tree squirrels of the world. To determine if this phenomenon was evident in other mammals a search was made of the literature concerning litter size of mammals of North America.

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Methods

The data were grouped according to closely related species because there were not enough data to test the hypothesis statistically for any single species although trends were apparent in several. Data concerning average litter size was preferred to data concerning range in litter size. However, for some groups where data were sparse, the median of the range in litter size was used and when this was done the latitude selected for the species was the median latitude for the range of the species as illustrated in Burt and Grossenheider (1952). Embryo counts alone were used because of the possibility that placental scars would not show resorption.

For those groups in which adequate data were available the slope of the regression was calculated by the method of least squares, and the coefficient of correlation was calculated and tested by the t test. For purposes that will become apparent with the progress of this

Table I.—Sources of litter size for species

Species	Source	Species	Source	Species	Source
Sylvilagus		*M. californicus*	Greenwald (1956)	*S. niger*	Brown and Yeager
floridanus	Negus (1958)	*M. montanus*	Hall (1959)		(1945)
	Ecke (1955)	*M. townsendi*	Hall (1959)		Moore (1957)
	Schwartz (1942)	*M. longicaudus*	Hall and Kelson		Hoover and Yeager
	Trippensee (1935)		(1959)		(1953)
	Dalke (1942)	*M. mexicanus*	Hall and Kelson	*S. alberti*	Asdell (1946)
	Gerstell (1937)		(1959)	*S. gerrardi*	Asdell (1946)
	Allen (1938)	*M. pinetorum*	Hall and Kelson	*S. griseus*	Asdell (1946)
	Hamilton (1940)		(1959)	*S. apache*	Asdell (1946)
	Haugen (1942)	*M. quasiater*	Hall and Kelson	*Tamiasciurus*	
	Beule (1940)		(1959)	*douglasi*	Asdell (1946)
	Henderickson (1943)	*Peromyscus*		*T. fremonti*	Asdell (1946)
	Bruna (1951)	*maniculatus*	Coventry (1937)	*T. hudsonicus*	Asdell (1946)
	Lord (1958) (1960)		Scheffer (1924)	*Glaucomys volans*	Asdell (1946)
S. aquaticus	Hunt (1959)		Jameson (1953)	*G. sabrinus*	Asdell (1946)
	Lowe (1958)		Howard (1949)	*Eutamias amoenus*	Asdell (1946)
S. auduboni	Sowls (1957)		Asdell (1946)	*E. cinericollis*	Asdell (1946)
	Hall (1959)	*P. leucopus*	Davis (1956)	*E. dorsalis*	Asdell (1946)
S. idahoensis	Hall (1959)		Coventry (1937)	*E. minimus*	Asdell (1946)
S. bachmani	Hall (1959)		Asdell (1946)	*E. quadrivattus*	Asdell (1946)
S. nuttali	Hall (1959)	*P. boylii*	Jameson (1953)	*E. townsendi*	Asdell (1946)
Microtus		*P. californicus*	Asdell (1946)	*Tamias striatus*	Asdell (1946)
pennsylvanicus	DeCoursey (1957)	*P. eremicus*	Asdell (1946)	*Lepus arcticus*	Hall (1959)
	Smith and Foster (1957)	*P. trueii*	Asdell (1946)	*L. americanus*	Adams (1959)
	Coventry (1937)	*P. gossypinus*	Pournelle (1952)	*L. townsendi*	Hall (1959)
	Goin (1943)	*Sciurus*		*L. californicus*	Asdell (1946)
	Harris (1953)	*carolinensis*	Asdell (1946)		Lechleitner
	Asdell (1946)		Uhlig (1956)		(1959)
M. chrotorrhynus	Coventry (1937)		Brown and Yeager	*L. alleni*	Asdell (1946)
M. ochrogaster	De Coursey (1957)		(1945)	*Sorex fumeus*	Asdell (1946)
	Hall (1959)			*S. longirostris*	Asdell (1946)

TABLE I.—(continued)

Species	Source	Species	Source	Species	Source
S. palustris	Asdell (1946)	*T. bulbivorus*	Asdell (1946)		Layne (1958)
S. arcuticus	Asdell (1946)	*T. douglasi*	Asdell (1946)		Layne and McKeon (1956)
S. cinereus	Asdell (1946)	*T. talpoides*	Asdell (1946)		Richards and Hine (1953)
S. dispar	Asdell (1946)	*T. townsendi*	Asdell (1946)		Gier (1947)
S. obscurus	Asdell (1946)	*Neotoma albigula*	Hall (1959)		Sullivan (1956)
S. vagrans	Asdell (1946)	*N. cinerea*	Asdell (1946)	*Alopex berengarius*	Asdell (1946)
Cryptototis parva	Asdell (1946)	*N. desertorum*	Asdell (1946)	*A. pribilofensis*	Asdell (1946)
Microsorex hovi	Asdell (1946)	*N. floridanum*	Asdell (1946)	*A. lagopus*	Asdell (1946)
Notiosorex crawfordi	Asdell (1946)	*N. lepida*	Asdell (1946)	*Vulpes velox*	Asdell (1946)
Blarina brevicauda	Asdell (1946)	*N. magister*	Asdell (1946)	*Martes americana*	Asdell (1946)
B. telmalestes	Asdell (1946)	*N. mexicana*	Asdell (1946)	*M. pennanti*	Asdell (1946)
Spermophilus (Citellus) parryi	Asdell (1946)	*N. micropus*	Asdell (1946)	*Mustela vison*	Asdell (1946)
S. tridecemlineatus	Asdell (1946)	*Vulpes vulpes* =(*fulva*)	Scott, T. G. (unpublished)	*M. frenata*	Asdell (1946)
S. townsendi	Asdell (1946)		Sheldon (1949)	*M. rixosa*	Asdell (1946)
S. tereticaudus	Asdell (1946)		Schofield (1948)	*M. cicognani*	Asdell (1946)
S. franklini	Asdell (1946)		Switzenburgh (1950)	*Taxidea taxus*	Asdell (1946)
S. harrisi	Asdell (1946)		Layne and McKeon (1956)	*Gulo luscus*	Asdell (1946)
S. beldingi	Asdell (1946)		Hoffman and Kirkpatrick (1954)	*Lutra canadensis*	Asdell (1946)
S. mohavensis	Asdell (1946)		Richards and Hine (1953)	*Mephitis mephitis*	Asdell (1946)
S. idahoensis	Asdell (1946)		Gier (1947)	*M. macroura*	Asdell (1946)
S. lateralis	Asdell (1946)		Sheldon (1949)	*Spilogale putorius*	Asdell (1946)
S. leucurus	Asdell (1946)	*Urocyon cinereoargenteus*	Wood (1958)	*Felis concolor*	Asdell (1946)
S. richardsonii	Asdell (1946)			*F. pardalis*	Asdell (1946)
S. spilosoma	Asdell (1946)			*F. onca*	Asdell (1946)
S. variegatus	Asdell (1946)			*Lynx rufus*	Asdell (1946)
S. washingtoni	Asdell (1946)			*L. canadensis*	Asdell (1946)
Geomys breviceps	Asdell (1946)			*Rattus norvegicus*	Davis (1953)
	Wood (1949)			*R. rattus*	Davis (1953)
Thomomys bottae	Asdell (1946)				

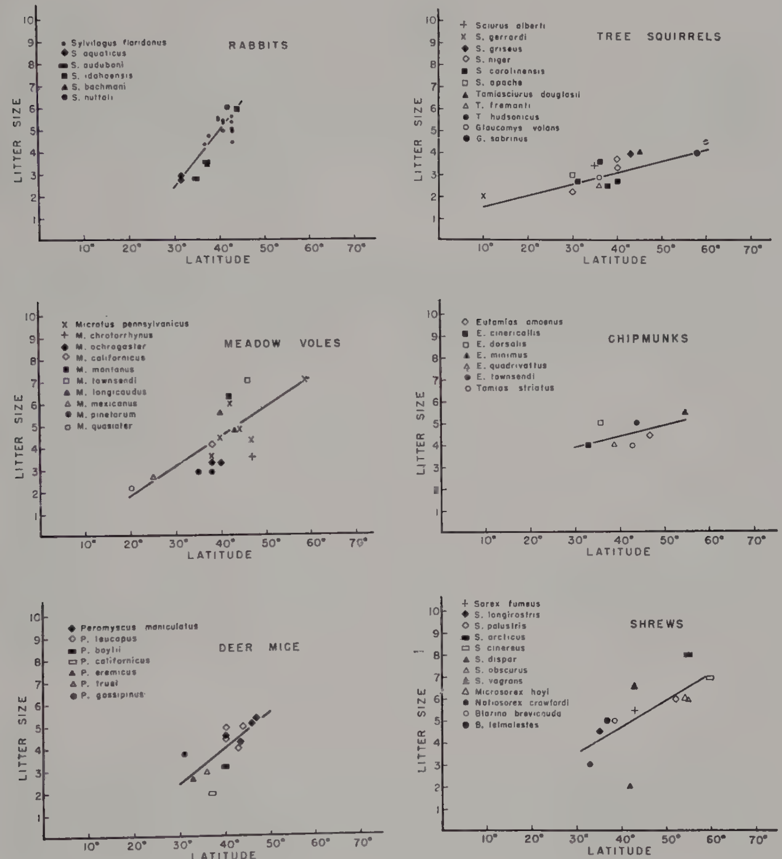

Fig. 1.—Mammals which showed a statistically significant positive correlation of litter size with latitude.

paper, the groups were arranged into three categories: prey species that do not hibernate, prey species that do hibernate, and predatory species. Table I lists the reference according to species from which the litter size data were obtained.

To test the consistency of the findings obtained from such a wide variety of sources which were probably collected by a variety of methods, the data from eight years of the North American Census of Small Mammals (Calhoun and Arata, 1950-1957) were analyzed for the relation of litter size to latitude in closely allied species. The data obtained from this source were all obtained from a standardized trap census.

OBSERVATIONS

NON-HIBERNATING PREY SPECIES

RABBITS

Twenty-one observations of six species of the genus *Sylvilagus* plotted a positive regression (m = 0.251) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.83, which was significant by the *t* test at the 0.1 per cent level.

MEADOW VOLES

Eighteen observations of ten species of the genus *Microtus* plotted a positive regression (m = 0.133) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.69, which was significant at the 1 per cent level.

DEER MICE

Fourteen observations of seven species of the genus *Peromyscus* plotted a positive regression (m = 0.160) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.66, which was significant at the 1 per cent level.

WOOD RATS

Seven observations of as many species of the genus *Neotoma*, based on the median of the range of the litter size and the median latitude of the range of the species, showed a positive regression (m = 0.086) of litter size with latitude. The correlation coefficient was 0.54, which was not significant.

TREE SQUIRRELS

Ten observations of ten species of the genera *Sciurus* and *Tamiasciurus*, based on the median of the range of the litter size and the median latitude of the range of the species, plotted a positive regression (m = 0.052) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.80, which was significant at the 1 per cent level.

CHIPMUNKS

Seven observations of seven species of the genera *Eutamias* and *Tamias*, based on the median of the range of the litter size and the median latitude of the range of the species, plotted a positive regression (m = 0.049) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.50, which was not significant, probably because of the small sample.

HARES

Five observations of five species of the genus *Lepus*, based on the median of the range of the litter size and the median latitude of the range of the species, plotted a positive regression (m = 0.091) of litter size with latitude. The correlation coefficient was 0.66, but was not significant due to the small sample.

SHREWS

Twelve observations of as many species of the genera *Sorex, Microsorex, Notiosorex* and *Blarina,* based on both mean and median litter size and the median latitude of the range of the species, plotted a positive regression (m = 0.120) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.65, which was significant at the 1 per cent level.

NORWAY RATS

Twenty-five observations of the species (*Rattus norvegicus*) plotted a positive regression (m = 0.027) of litter size with latitude. The correlation coefficient for this group was 0.26, which was not significant. However, thirty-two observations of this species plotted a positive regression (m = 0.45) of the prevalence of pregnancy (per cent of a sample of females that were pregnant) with latitude. The correlation coefficient for this group was 0.35, which was significant at the 5 per cent level.

ROOF RATS

Nine observations of the species (*Rattus rattus*) plotted a positive regression (m = 0.049) of litter size with latitude. The correlation coefficient for this group was 0.69, which was significant at the 5 per cent level. In this same species, fifteen observations plotted a negative regression (m = -0.18) of the prevalence of pregnancy with latitude. The correlation coefficient for this group was 0.20, which was not significant.

HIBERNATING AND FOSSORIAL PREY SPECIES

GROUND SQUIRRELS

Fifteen observations of as many species of the genus *Spermophilus* (*Citellus*), based on the median of the range of the litter size and the median latitude of the range of the species, plotted a regression of nearly zero (m = 0.009) with latitude (see Fig. 2). The correlation coefficient was 0.06, which was not significant.

POCKET GOPHERS

Six observations of six species of the genera *Geomys* and *Thomomys,* based on both mean litter size and the median of the range of the litter size and the median latitude of the range of the species, plotted a nearly zero (m = 0.018) regression with latitude (see Fig. 2). The correlation coefficient was 0.14, which was not significant.

PREDATORS

RED FOX

Fourteen observations of this species (*Vulpes vulpes = fulva*), based on mean litter size as determined by 14 studies of the species at different locations in the United States, plotted a negative regression (m = −0.289) of litter size with latitude (see Fig. 2). The correlation coefficient for this species was 0.41, which was not significant.

Gray Fox

Six observations of this species (*Urocyon cinereoargenteus*), based on mean litter size, plotted a slightly negative regression (m = –0.029) of litter size with latitude (see Fig. 2). The correlation coefficient for this species was 0.36, which was not significant.

Foxes

Six observations of six species of the genera *Alopex, Vulpes* and *Urocyon,* based on the median of the range of the litter size and the median latitude of the range of the species, plotted a positive regression (m = 0.078) of litter size with latitude (see Fig. 2). The correlation coefficient for this group was 0.60, which was not significant.

Mustelids

Twelve observations of as many species of the genera *Martes,*

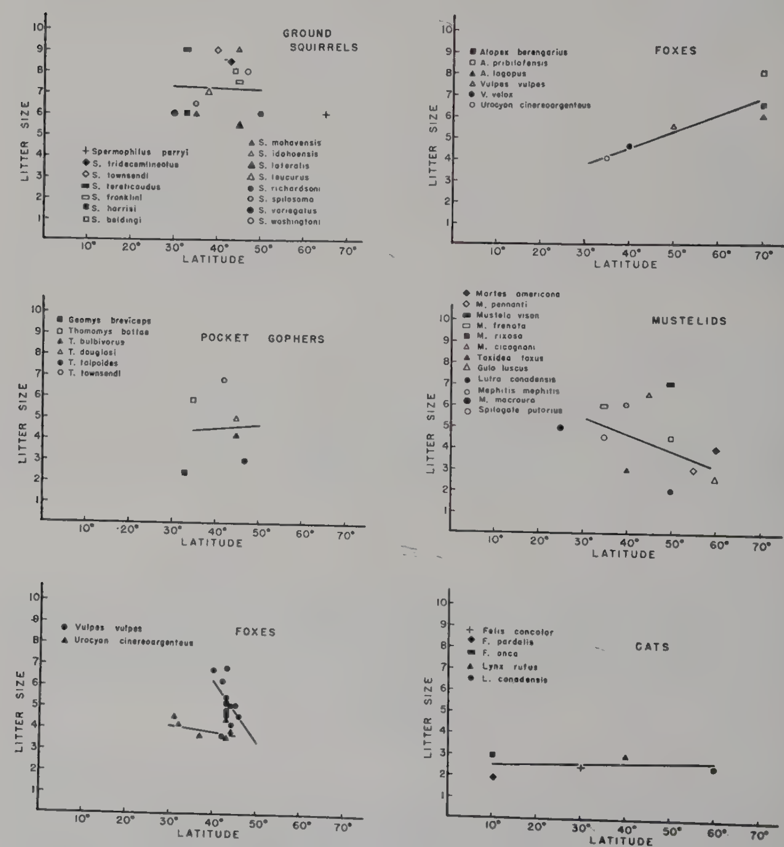

Fig. 2.—Mammals which showed no significant correlation of litter size with latitude.

Mustela, Taxidea, Gulo, Lutra, Mephitis and *Spilogale* based on the median of the range of the litter size and the median latitude of the range of the species, plotted a negative regression (m = –0.061) of litter size with latitude (see Fig. 2). The correlation coefficient for this group was 0.32, which was not significant.

CATS

Five observations for as many species of the genera *Felis* and *Lynx,* based on the median of the range of the litter size and the median latitude of the range of the species (in North America), showed no regression (m = 0.003) of litter size with latitude (see Fig. 2). The correlation coefficient for this group was 0.11, which was not significant.

NORTH AMERICAN CENSUS OF SMALL MAMMALS

From the data compiled by Calhoun and Arata (1950-1957) only two genera, *Peromyscus* and *Microtus,* contained sufficient material for statistical analysis of the relation of embryo counts to latitude. In the genus *Peromyscus* twenty-four observations plotted a positive regression (m = 0.089) of litter size with latitude. The correlation coefficient for this group was 0.59, which was significant at the 1 per cent level. In the genus *Microtus* seventeen observations plotted a positive regression (m = 0.075) of litter size with latitude. The correlation coefficient for this group was 0.53, which was significant at the 5 per cent level.

DISCUSSION

It is apparent from the observations that only a certain portion of the groups examined fulfilled the expectations of the thesis of this paper. Only the non-hibernating prey species seem to have increasingly larger litters which approach toward the polar region. Both the hibernating and fossorial prey species and the predators, with the possible exception of the foxes, appear to be unaffected by latitude with reference to litter size.

The role of hibernation in this phenomenon appears to be supported by the tree squirrels, chipmunks and wood rats, all of which are partial hibernators; that is, they are known to remain in their holes or nests during periods of extremely adverse weather during the winter. These same species showed a lower gradient of increase of litter size with increase in latitude.

The plain implication is, that whatever the factor is that is working on these animals, be it compensation for high mortality or something else, it is operating in the winter upon those prey species which are exposed. And just as plainly it appears not to affect the predators, except possibly the foxes.

The foxes present a puzzling situation. There appears to be a positive relation between litter size and latitude when the four species of fox found in North America are compared. But there happens to be much literature available on embryo counts of foxes made by many

workers in different parts of the United States. These data actually show a reverse or negative relationship between litter size and latitude in the red fox. While this relationship was not statistically significant, a study by Schofield (1957) showed a significant difference in litter size of red foxes between the Upper Peninsula, the northern Lower Peninsula, and the southern Lower Peninsula of Michigan. In this case litter size became successively larger from north to south. Layne (1956) found different litter sizes in three regions of New York state, but here the region with the largest litters was located between the regions with successively smaller litters. Both in New York and in Michigan the litter size of the red foxes appears to be inversely related to the density of breeding populations of foxes which in Michigan was dependent on human predation.

In the case of mustelids, the necessity to combine so many different genera to obtain a sufficient number of observations for statistical treatment may have resulted in the apparent lack of correlation between litter size and latitude in this group. However, no closely related group within this family, such as the skunks, showed any tendency to exhibit a correlation.

Lack (1946) described a similar phenomenon in birds, that is, larger clutch size in high latitudes. In birds the explanation appears to be related to their ability to secure more food for their young due to the greater day length. In mammals it is difficult to believe that the increased day length would have any positive relation to the increased litter size, because many of the groups are inherently nocturnal and are actually forced to seek food in the light due to the long arctic summer day. The apparent lack of response of the hibernators and the predators also would be inexplicable by this theory. More explicable is the theory that the increased litter size is directly related to the mortality sustained by the species. This is a rather universal phenomenon and its application here is only slightly different from its more traditional applications. One possible explanation of the method through which it operates is provided by the work by Christian and Lemunyan (1957) which showed smaller litters in the more dense breeding populations. Thus the hibernators, which escape the severe mortality of the winter, emerge in the spring with relatively greater population densities than the non-hibernating species. Therefore, the hibernators should have relatively smaller average litters. Farther south the winters are milder and presumably the winter mortality among non-hibernators is lower, resulting in more dense spring breeding populations and thus, smaller average litters

However, the severity of the winter weather in the higher latitudes has probably been a force for selecting animals with large litters.

The test of the consistency of the findings from the varied sources by analysis of the data from the North American Census of Small Mammals again found a positive correlation between litter size and latitude in both *Peromyscus* and *Microtus*.

The data compiled by Davis (1953) for both Norway and Roof

rats contained information concerning prevalence of pregnancy in addition to litter size data. Analysis of this information showed a significant positive correlation between prevalence of pregnancy and latitude in the Norway rat but not in the Roof rat. Both species showed positive correlation of litter size with latitude although the coefficient of correlation was significant for the Roof rat only. Thus, it is apparent that those forces which are correlated with latitude that cause the increase in litter size with increasing latitude might also cause an increase in the prevalence of pregnancy.

Workers interested in investigating this phenomenon more thoroughly should make periodic collections throughout the breeding season as frequently as the length of the gestation period of the species being investigated. Data should be collected concerning both prevalence of pregnancy and average litter size. Analysis of data collected in this manner can give the mean annual production of young per female.

SUMMARY

Analysis of the data concerning litter size in relation to latitude in North American mammals has shown statistically significant positive correlation for six groups of closely related non-hibernating prey species. Two groups of hibernating and fossorial prey species and the predators, with the possible exception of the foxes, showed no relation between litter size and latitude. Possibly the relation reported by other workers between mortality and reproduction is, at least in part, dependent on an inverse relationship between density of breeding adults and litter size. Also the severity of the winter weather in the higher latitudes has probably been a selective force for larger litters.

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Notes and Discussion

A Northernmost Record of Plecotus rafinesquii Lesson (Mammalia, Chiroptera).

The previous northernmost record of a species of *Plecotus* for the eastern United States was based upon a specimen collected five miles southwest of Greencastle (Putnam County), Indiana (A. W. Butler, 1895, Proc. Indiana Acad. Sci. for 1894:86). Butler's specimen is presumably lost and there has been some doubt among mammalogists as to which species this record should be referred. Hall and Kelson (The Mammals of North America, p. 200, 1959) referred the record to *P. townsendii virginianus* (Handley). On the other hand, Handley (Proc. U. S. Nat. Mus., 110:165, 1959) believed it to be referable to *P. rafinesquii rafinesquii* Lesson.

On December 13, 1959, I collected a male of Rafinesque's big-eared bat, *P. rafinesquii,* from a concrete conduit along Indiana Highway 43, 1.3 miles north of West Lafayette (Tippecanoe County). The conduit is in a wooded area and empties into the Wabash River some 700 feet away. The bat was hanging from the ceiling of a side shaft 137 feet from the nearest outside opening.

Over the past three winters, the conduit had been checked 42 times in studying hibernation in a small group of the big brown bat, *Eptesicus fuscus* (Palisot de Beauvois). This is the first bat of another species to be found. The most recent trip, prior to December 13, was on December 6, at which time only two individuals of *E. fuscus* were present.

This is the sixth time, including Butler's record, that this bat has been collected in Indiana. It extends the known range by 59 miles from the previous northernmost record of a species of *Plecotus* in the eastern United States and by 120 miles from the previous northernmost record of *P. r. rafinesquii* based upon an extant specimen. This collection falls into a pattern noted by Handley (*op. cit.*: 157); that is, that all northern specimens have been taken or recorded in caves or cave substitutes during the cooler months of the year.

The specimen (No. NW 248 in my collection) had the following measurements: total length, 104 mm; tail, 48 mm; hind foot, 10 mm; ear, 35 mm; tragus, 13 mm; forearm, 45 mm; wingspread, 305 mm; and testes 2 x 4 mm. It weighed 10.5 grams with considerable subcutaneous fat present in the inguinal and lower back region. The stomach contained several specimens of the nematode, *Capillaria palmatus* Chandler (U. S. Nat. Mus. Helm. Coll. No. 56620), identified through Doctor Allen McIntosh of the Animal Disease and Parasite Research Branch, U. S. Department of Agriculture.—Nixon Wilson, Department of Entomology, Purdue University, Lafayette, Indiana.

A Congenital Diaphragmatic Hernia in the Raccoon

A captive group of raccoons (*Procyon lotor*) has been maintained for research purposes in Urbana, Illinois, since the fall of 1956. On April 15, 1959, a female, bred in captivity, gave birth to a litter of three males which were removed from their mother on June 9, 1959, and reared together in another cage.

On July 7, 1959, one of the males was castrated in order to study the

effects of castration on the maturation rate of the skeleton. This operation caused no decline in growth of the animal or other apparent ill effects.

This male was found dead in the cage on September 30, 1959. He was in good physical condition and weighed 7.1 lbs., while his litter mates weighed 7.5 and 6.4 lbs., respectively. At autopsy the entire stomach and approximately four inches of the duodenum were found in the left thoracic cavity. The stomach and duodenum apeared to be normal; there were no signs of strangulation of the duodenum, no adhesions, and no indication of rupture or inflammation around the small hole in the diaphragm through which the stomach and duodenum had entered into the thoracic cavity. The raccoon showed no other obvious signs of illness and otherwise appeared to be in good health. It appears that he died of suffocation when the stomach entered the thoracic cavity and put pressure on his lungs. Because of the points just mentioned, plus the fact that body weight was normal, the hernial opening is believed to be congenital; but the stomach and duodenum probably remained in their normal positions until a short time prior to death. Lung, stomach and intestinal tissue of the raccoon were not congested, indicating that he probably died within minutes after the stomach entered the thoracic cavity.

According to Secord, most cases of acquired diaphragmatic hernia in the dog occur as a result of injury (*Canine Surgery,* Amer. Vet. Publs., Inc., 4th ed. 1957:404). However, the cages in which the raccoons were kept were protected by a high wire fence with a locked gate so it is unlikely that this male was injured by humans or animals outside the cage.

Because he was reared with his litter mates there is little chance that there was any injury because of the normal playing and "fighting" among the young raccoons in their cage. Although Secord reports that being run over by an automobile is the most common direct cause of diaphragmatic hernia in the dog, he does indicate that some cases in young puppies and kittens are congenital. Most of such animals are stunted with the stomach permanently lodged in the thoracic cavity. This author also states that in a left-sided hernia involving the stomach, death may be caused by asphyxiation because of the pressure on the lungs from the bloated stomach.

R. M. Thomas, D.V.M., Instructor of Veterinary Pathology and Hygiene, University of Illinois, College of Veterinary Medicine, also examined this animal and confirmed this diagnosis.—GLEN C. SANDERSON, Illinois Natural History Survey, Urbana.

Eleocharis elliptica and E. compressa: Further Notes and Corrections

When the authors in their recent study of *E. compressa* and *E. elliptica* (Am. Midl. Nat. 63:143-148. 1960) combined these two taxa into the same species, we erroneously stated that *E. compressa* had priority over *E. elliptica.* However, *E. elliptica* Kunth (1837) clearly antedates *E. elliptica* Sullivant (1842). This lapse has kindly been called to our attention by Dr. E. G. Voss.

As a result of this, typical material of *E. elliptica* should be known as *E. elliptica* Kunth var. *elliptica,* while the specimens with compressed culms should be made a further variety of *E. elliptica.* The question then arose as to the varietal epithet that should be used. It happens that there is already a varietal epithet in *E. compressa:* var *atrata* Svenson. It then became necessary to examine the type collection of var. *atrata.*

Svenson named var. *atrata* from a specimen collected by Pease (No. *12991*) from Presque Isle, Pennsylvania. The authors wish to thank Dr. Clarence Kobuski of the Gray Herbarium for kindly loaning the specimen.

After a careful study of the type (there are three specimens on the sheet), it was clear that here we were dealing with a plant much more closely related to *E. elliptica* than to *E. compressa.* Two of the three specimens had 6 vascular bundles per culm while the third specimen possessed 8. The scales of each plant were deep purple-brown (not blackish) while the basal sheaths were reddish. No differences could be observed in achene characters.

Although Fernald (Gray's Manual of Botany. 8th ed. 1950. Pg. 258) gives the range for var. *atrata* as "shores of Great Lakes," etc., a recheck of Illinois material shows plants with scale color identical to the type specimen as occurring throughout Illinois. The color of the basal sheaths varies with these dark-scaled specimens.

In re-evaluating the situation, the taxon *E. compressa* var. *atrata* seems nothing more than a dark-scaled form of typical *E. elliptica. Eleocharis compressa* may then be known as var. *compressa* of *E. elliptica.*

The citation for these taxa should be corrected to:

ELEOCHARIS ELLIPTICA Kunth var. ELLIPTICA

Eleocharis elliptica Kunth, Enum. 2:146. 1837.

Eleocharis capitata var. *borealis* Svenson in Rhodora 34:202. 1932.

Eleocharis tenuis var. *borealis* (Svenson) Gleason in Phytologia 4:22. 1952.

Eleocharis compressa var. *borealis* (Svenson) Drapalik & Mohlenbrock, Am. Midl. Nat. 63:147. 1960, nomen illeg.

ELEOCHARIS ELLIPTICA Kunth var. ELLIPTICA f. ATRATA (Svenson) Drapalik & Mohlenbrock, comb. nov.

Eleocharis compressa var. *atrata* Svenson in Rhodora 34:218. 1932.

ELEOCHARIS ELLIPTICA Kunth var. COMPRESSA Drapalik & Mohlenbrock, stat. nov.

Eleocharis compressa Sulliv. in Am. Jour. Sci. 42:50. 1842.

—DONALD J. DRAPALIK and ROBERT H. MOHLENBROCK, Southern Illinois University, Carbondale.

American Institute of Biological Sciences Translation Program

The American Institute of Biological Sciences is currently translating and publishing seven Russian research journals in biology. These journals are translated with support from the National Science Foundation, which is eager that such information be more widely distributed to biologists throughout the world. It is hoped that this material will aid biologists in research, prevent duplication of work, give some idea of the work being done by Soviet scientists in the field of biology, and also bring about a better international understanding among scientists.

Because of the support of the National Science Foundation, the AIBS can offer these translations at a fraction of their publication cost, with even further price reduction to AIBS members and to academic and non-profit libraries. This reduction, the AIBS feels, places the translation within the reach of all biologists.

The journals currently being translated are: *Doklady:* Biological Sciences Section; *Doklady:* Botanical Sciences Section; *Doklady:* Biochemistry Section; *Plant Physiology; Microbiology; Soviet Soil Science;* and *Entomological Review.*

In addition to its program of Russian Biological Journal translations, the AIBS has instituted a separate program of translation and publication of selected Russian Monographs in biology.

It was felt that the program of Journal translations was not sufficient

to cover all of the significant work being done in all fields of biology by Russian scientists. With the aid of competent authorities, the AIBS has translated and published six Russian monographs and one monograph is in the process of being published. In addition, several prominent monographs in various biological areas are being considered by the AIBS and the National Science Foundation for translation and publication. The monographs that have been published are: Origins of Angiospermous Plants by A. L. Takhtajan; Problems in the Classification of Antagonists of Actinomycetes by G. F. Gauze; Marine Biology, Trudi Institute of Oceanology, Vol. XX, edited by B. N. Nikitin; Arachnoidea by A. A. Zakhvatkin; and Arachnida by B. I. Pomerantzev. The manuscript for Plants and X rays by L. P. Breslavets is in the final stages of preparation and should be published early in 1960.

Additional information pertaining to this program may be obtained by writing to the American Institute of Biological Sciences, 2000 P Street, N. W., Washington 6, D. C., U. S. A.

Book Reviews

THE RUSTY LIZARD. A POPULATION STUDY. W. Frank Blair. University of Texas Press, Austin. 1960. xiv+183; 31 Figs. $4.50.

This book on *Sceloporus olivaceus* is one of the most significant studies of a natural population of vertebrates, easily equalling in scope and importance the classic reptile studies of Fitch in North America and of St. Girons and Volsøe in Europe. Dr. Blair's study is of particular note ecologically because it covers a five-year period during one of the severest droughts in history in central Texas. It has often been stated that consideration of extreme conditions is most important in studies of adaptation and evolution; in this investigation data are presented on the mechanisms by which this population was able to maintain its numbers during a period of climatic extremes.

Basically, the book deals with the populations dynamics of this arboreal lizard on a ten-acre tract near Austin, Texas. Approximately 3000 lizards were trapped, noosed, or collected by hand and marked in various ways for individual indentification in order to follow their dispersion, home range establishment, growth, reproduction and mortality. The environment of the lizards is described in detail including such aspects as vegetation and vegetational changes, actual or potential predators, possible competitors and food supply.

Most of the significant data are included in two chapters dealing with adaptation by the individual and adaptation by the population. In the first of these mating, growth rate, loss and regeneration of the tail, ontogenetic pattern changes, body temperature, diel cycle and escape behavior are the fundamental topics considered. No new generalizations or phenomena are reported, but excellent information on growth from numerous recoveries of marked animals over long periods is made available. My only criticism of this section is of what appears to be a lack of balance between the topics. For example, temperatures were obtained apparently of only a dozen lizards during the study and less than a page is devoted to this aspect of lizard ecology; in contrast, 11½ pages and a number of tables are devoted to tail growth and regeneration—more pages than are devoted to growth of the individual.

The chapter dealing with adaptation by the population is concerned primarily with how the breeding population of adults was maintained during the adverse period covered by the study. Most mortality was due to nest failure and loss of juveniles for several reasons. Very little effect was noted from food shortage which seemed to play a minor role in the ecology of these lizards. The population of breeding adults remained fairly constant due in part to an extremely high (for reptiles) reproductive potential and in part to an apparently greater percentage survival of young lizards during seasons when population density and reproduction were low than when density and egg production were high. Too, immigration plays some part in stabilizing the density of lizards.

The last part of the book concerning organization of the population contains material on sex ratios, movement and dispersal, home ranges and social interactions. It appears that the sex ratio, unbalanced in favor of females in the older age classes, is an adaptation for obtaining maximum reproduction in a promiscuous mating system. One male can fertilize several females and a disparate sex ratio removes older males from intraspecific com-

petition with the reproductive element of the population. Home ranges, once established, remain fairly stable for years and are organized around suitable trees, the availability of which appears to set the upper limit for the adult population.

Only one omission of data that might have been obtained was evident to this reviewer. Number of layings per season are reported, as is mating behavior and copulation, but there is no information of whether or not each laying is preceded by mating or whether one mating is sufficient for an entire reproductive season. Similarly, data are absent on elapse of time between copulation and laying which might give some indication of the time of preovipositional development. However, these omissions in no way detract from an excellent study. It would be naive to expect that every phase of life history could be covered by any one study and certainly the most significant aspects are treated thoroughly.

The format and print of the book are attractive and the figures and tables, with a few exceptions, are clear and well done. The book is inexpensive and essential for every herpetologist interested in the broader aspects of his field and can be unreservedly recommended for any student of population ecology.—DONALD W. TINKLE, Department of Biology, Texas Technological College, Lubbock.

A CALIFORNIA FLORA. By Philip A. Munz in collaboration with David D. Keck. University of California Press, Berkeley and Los Angeles. 1959. 1,681 pp., frontispiece, 134 text figures. $11.50.

This book which skillfully brings together the contributions of numerous special studies of Californian plants since the last manual of the state was published by Jepson in 1925 deserves laudatory comment. At the same time, it should be emphasized that it is not merely a compilation of the work of others but represents a careful evaluation of the various groups from extensive herbarium study and field experience. All of us who have been looking for such a volume for a number of years can be grateful to have it actually on hand.

In scope it includes all of the vascular plants known to grow spontaneously in California, and omits the nonvascular plants. More than 5500 species are described, which is an increase of about 1500 over the number listed by Jepson 35 years ago.

The most conspicuous deviations from current floras in the United States are the names given to the divisions, the delimitation of certain families, and the sequence of families, all of which reflect recent information and evaluation of the major categories and their relationships. The sequence of families may be disturbing to some who are accustomed only to the Englerian system used in most floras and herbaria in this country, but for some of the rest of us who have never taken any sequence too seriously, the present departure from tradition is refreshing and desirable, if only to indicate that no sequence should be considered sacred. For those who may have difficulty locating families with the arrangement used and find the index cumbersome for this purpose, an alphabetical list of families with appropriate page references (which can be pasted conveniently on the inside of the back cover) is available on request from the Rancho Santa Ana Botanic Garden, Claremont, California. I have found this supplementary index to be extremely convenient.

The twenty pages of introductory material are a contribution in themselves for they serve not only to orient the user of this volume but also

provide the general reader with a concise introduction to the diversity of the vegetation of California and its historical development, with the latter in the form of a very elegant and authoritative summary by Daniel I. Axelrod. The section on plant communities provides an effective and desirable basis for indicating the habitat of each species. A list of species is given for each of the plant communities but no distinction is made between species that are widespread and conspicuous elements and those that are local or relatively minor associates.

The illustrations, except for the colored frontispiece of California poppy, are limited to line drawings of good quality in a banner at the beginning of each family. The few plants illustrated have been selected to represent the most characteristic traits of the family as it occurs in California.

The descriptions in general seem to be adequate, although the treatment of polytypic species is somewhat confusing until one realizes that the description, range of distribution, and ecological association given for the "species" is in fact pertinent only to the subspecies or variety which includes the nomenclatural type of the species. Subspecies, which are of equivalent taxonomic rank, are then appended, often following a key to the subspecies (or varieties). Even then, the subspecies which includes the type is shown as being the "species," which has the effect of suggesting that the subspecies which happened to be first described is of greater importance than those subsequently discovered. Chromosome numbers are given for each taxon, and while some reports have been overlooked and no bibliography of the citations is given, the chromosome information is a welcome addition to the descriptions.

Professional botanists will have every reason to generally commend this book as a reference for their own use and for the use of other experienced botanists. On the other hand, some of us had hoped that this volume would also be a boon to instruction in identification of the native flora. Having now used it in a field botany class for a semester, I must say regretfully that it not only falls short of my hopes, but has proved discouraging to students who were initially enthusiastic at the prospect of learning to identify plants. The reasons for this are twofold. In the first place the weight of the book (about 4 lbs.) and the complexity of the keys necessary to treat such a diverse flora as that of California make it unwieldy. The necessary use of thin paper makes the pages all but unmanageable in a breeze; the large number of species and genera included requires the novice and even students of considerable experience to spend a discouraging amount of time identifying an unknown plant. For teaching purposes a regional flora of more limited scope, such as the earlier *Manual of Southern California Botany* by Munz (1935), is much to be preferred, but unfortunately this book has been out of print for a number of years.

Although the very magnitude of the *Flora* is discouraging to the student, the second basis on which they have become frustrated and have condemned it in no uncertain terms is the prevalence of innumerable typographical errors or errors in the construction of the keys which not only prevents them from identifying many plants but leaves them uncertain even when they have arrived at a reasonable answer. I do not recall a single class exercise in which some unnecessary obstacle such as omitted lines or names, interchanged lines in the keys, inconsistencies between the keys and descriptions, has not plagued the students. The professional botanist will not run into most of these frustrations for he will recognize the genus *Prunus* on sight and will not discover that it must have five carpels in order to be identified as that genus in the key to the genera of Rosaceae; he will recognize that *Erodium* belongs to the

Geraniaceae without realizing that species with pinnate leaves cannot be identified in the key to the families. On the other hand, the student rapidly loses confidence when he runs into such errors or omissions, and there is no way to reassure him. Even the professional will be disconcerted by some of the errors such as finding the same taxon described as both *Pellaea compacta* and *Pellaea mucronata* var. *californica,* with each cited as a synonym of the other.

I understand that some of the omissions, inverted type etc., are being corrected for the next binding, but what is needed is an immediate reprinting after a very careful scrutiny of the entire book with a view to correcting all errors. It is unexcusable for the University of California Press to issue a book of high scholarly merit, and an outstanding contribution to its field, which because of poor editing and proofreading has the effect of discouraging students and preventing them from gaining knowledge and intellectual satisfaction from its use.—HARLAN LEWIS, University of California, Los Angeles.

THE VEGETATION OF WISCONSIN: AN ORDINATION OF PLANT COMMUNITIES. By John T. Curtis. xi, 657 pages and 270 maps, charts, tables and original photographs. The University of Wisconsin Press, Madison, Wisconsin. 1959. $7.50.

When a book of over 650 pages is written about the vegetation of any region, it is a significant addition to the rather limited literature on this little-studied topic. When this book concerns itself with the vegetation of but one of the fifty United States, we might reasonably anticipate that it would probe deeply into the subject; Dr. Curtis' book is not a disappointment. Specialists who have kept abreast of developments in vegetation study in the past decade — and especially the significant published contributions of Dr. Curtis and his students and those of R. W. Whittaker — will find little that is new on the nature of vegetation. However, Dr. Curtis has woven together the descriptions and analyses of the myriad of Wisconsin's vegetation types into a very readable volume that will be highly informative to vegetation specialists as well as biologists, conservationists, agricultural specialists and intelligent laymen.

The book is divided into seven parts plus an appendix, glossary, bibliography, species list and index. The first part includes brief chapters on the flora, the environment, the plant communities and their distribution in Wisconsin and a chapter on vegetation study methods.

In the terse but well-done chapter on flora, the state is divided into a northern and a southern floristic province with a tension zone between. The following floral elements make up the state flora: Boreal, Alleghenian, Ozarkian, Prairie and Coastal Plain elements. An "epibiotic element" is made up of plants from various regions but surviving in Wisconsin on rock cliffs, lake shores, etc., and includes a Preglacial element surviving the Pleistocene in the Driftless Area. An exotic element includes primarily the weeds introduced by man.

The Preglacial element is singled out for special treatment and introduces a point on which Dr. Curtis would probably not find universal agreement among pleistocene biogeographers. On p. 14, he states, "A variety of geological, climatological and ecological evidence . . . strongly supports the hypothesis that the Driftless Area was at least partially covered with vegetation at all times and that it formed the source for the bulk of the plant cover which later spread out over the remaining parts of the state as these were deglaciated." And on

p. 11 ". . . that all of our major dominants survived the glacial advances in or near the non-glaciated region and subsequently spread from that center."

The vegetation treatment combines several approaches to vegetation classification. Perhaps the most characteristic aspect of the over-all treatment is that vegetation, at the outset, is approached as representing a continuous variable. Thus, the sub-divisions recognized are not discrete units but rather groupings of convenience which correspond in general with the vegetation patterns long recognized by observant field men. The community concept held is the individualistic community of Gleason and Ramensky. The primary categories are the three great physiognomic groups: forests, grasslands and savannas. In a category labeled "lesser communities" he variously uses physiognomy, physiography, species composition and land use for recognizing fen, meadow, bog, aquatic, beach, dune, cliff and weed communities. Floristic differences north and south of the tension zone lead to the northern forests, grasslands and savannas being considered as different vegetation types from their southern counterparts. The distinction takes place across the narrow tension zone which includes communities containing both floristic elements.

Dr. Curtis considers each of the major vegetation types as a continuum which was sampled extensively and without the usual bias of first deciding on the sub-units. Subsequent fractioning is accomplished from these data by recognizing more-or-less arbitrary segments along a linear arrangement of the stands. This arrangement is obtained by various computations and reflects primarily differing moisture relationships. Where the continuum is extensive and enough data available, five segments termed wet, wet-mesic, mesic, dry-mesic, and dry, respectively are discussed. By this procedure 21 major communities are recognized which together with the 13 "lesser communities" give Wisconsin a total of 34, each of which is discussed in varying detail.

The bulk of the text, part 2 through part 6, contains treatments of these 34 units. These discussions are not equally detailed since the amounts of available data are not equivalent. However, the author clearly states the degree of confidence to be assigned the various treatments.

In general the material includes a description of the composition and structure, often with excellent resumes of early accounts of the pre-settlement conditions of the type; life history sketches of some of the major species; successional relationships; associated biota; regional variations; associated environment; geographical relationships — both North America and European; origin of type; and utilization and current management of the type.

Following the individual treatments is part 7 titled, "The vegetation as a whole." It includes chapters on postglacial history, the effect of man on the vegetation and interrelations of communities. The latter chapter is of particular interest to the vegetation specialist and includes a well-written summary of the work of the author and his students on ordination of vegetation, the behavior of various non-dominant species on ordination diagrams, an inquiry into the validity of fidelity of species as a criterion for vegetation classification, and the author's conclusions concerning the nature of plant communities. These conclusions represent a vindication of the deep and precocious insight into vegetation published by H. A. Gleason and independently in Russia by Ramensky over three decades ago and essentially ignored by U.S. and European students of vegetation until recently.

One of the fine contributions of the book is the refreshing historical depth derived from a skilled use of well-chosen quotations of early observers.

Occasional wryly humorous jabs at narrowly trained technicians and bureaucratic dicta provide a light touch to serious problems. *E.g.* on p. 337, in discussing the changes taking place in the oak openings of the pre-settlement

savannas, he states, "These huge, open-grown trees tell a graphic story of an interesting phase of Wisconsin's history. It is unfortunate that many consulting foresters are so imbued with textbook silvicultural theory as to invariably recommend that forest owners remove these derisively named "wolf trees" so that more valuable (*sic*) trees may take their place. It is highly probable that an active appreciation of the history of their forests as dynamically changing biotic complexes would in the long run be of more value to the owners."

All individuals enlightened to the rapidity with which the last representative pieces of many of our natural areas are disappearing will find particularly gratifying the numerous passages following descriptions of interesting vegetation which state, "This stand has been set aside as a Scientific Study Area by the State Board for the Preservation of Scientific Areas." Although ecologists and others have long fought to preserve blocks of natural areas as continuous reservoirs of natural experiments, this book will show a degree of organized success in Wisconsin unmatched in most states.

Geographically oriented biologists will find valuable the numerous maps showing various environmental conditions, species ranges, pre-settlement boundaries of the major vegetation types, the location of the examples studied for each type, and maps for postglacial pollen diagrams. Vegetation specialists will be gratified to find an excellent appendix which consolidates recent data from significant published and unpublished vegetation studies in the state. For most types these data include dot maps of stand locations, maps of the pre-settlement extent of the type, average composition for the type, including both tree and ground layers where present, summaries of two typical stands for the type, and a resume including important vegetation, geographic, environmental and bibliographic statistics for the type.

The book is singularly free of the typographical and other errors that first printings usually have. One that is obvious occurs on p. 99, Fig. 10, where the ordination on the abscissa would appear to be from wet on the left through mesic in the center to dry on the right. However, the right hand end is labeled "M" as is the middle. Another, more bothersome point is the series of disagreements between the stated numbers of stands representing the study material. *E.g.*, Figure VIII-I shows approximately 108 dots for Southern Lowland Forest while table IV-2 shows 16 stands of Southern Forest-Wet and 64 stands of Southern Forest-Wet Mesic; on p. 133 the text mentions 127 Xeric forest stands, the dot map (Fig. VII-I) on p. 522 shows 110 dots and table IV-2 on p. 517 shows 30 stands for Southern Forest-Dry and 54 stands for Southern Forest-Dry mesic. Similar disagreements occur for Southern Mesic Forest, Northern Lowland Forest, Northern Mesic Forest, Northern Boreal Forest and Mesic Prairie. There is probably a good explanation for these differences but a note in the appendix would allay the readers' suspicion that an error in computation is the cause.

The type is large, the paper and binding of good quality, and the illustrations, well chosen. The vegetation photographs in particular form an attractive and useful part of the book. The glossary includes most terms likely to be unknown to the average educated reader. The bibliography covers 25 pages and includes publications of Australian, Canadian, British, German, Swedish, Polish, Russian, Dutch, French, Austrian, Japanese, Swiss, Danish, Norwegian and Finnish nationality, as well as a wide array of United States entries. An alphabetically arranged species list is included which designated the number of communities in which the species occurs and a symbol indicates the native community in which it achieves its maximum presence. The index is unusually complete, including page references for major species, vegetation types, authors, geographic names and the biological terms used.

In summary, this book is, in the reviewer's opinion, the best treatment of the vegetation of any of the 50 United States and will serve as a useful reference and guide for students of vegetation, biologists and others for many years. Its weaknesses stem primarily from the condition of man's current knowledge of the vegetation rather than from inadequacies of the author. —JOHN E. CANTLON, Michigan State University, East Lansing.

THE ANTECEDENTS OF MAN: An Introduction to the Evolution of the Primates. By W. E. Le Gros Clark. Quadrangle Books, Chicago. 374 pp., 152 figs. 1960. $6.00.

Contained in the pages of this book is the substance of the Munro Lectures presented at the University of Edinburgh in 1953. More recent findings have been added. Basically the book is similar to the author's *The Early Forerunners of Man* (1934). After informative opening chapters on the evolutionary process and brief biographies of fossil and contemporary primates with the erection of a primate family tree, there follow chapters on the comparative morphology of the dentition, skull, limbs, brain, special senses, digestive system, and reproductive system. The terminating chapter is a discussion of evolutionary radiations of the group.

The tree-shrews receive considerable attention. All the evidence for including them in the primates is carefully presented, and it seems conclusive. Modern primates receive more attention than do the relatively rare extinct forms. The comparative anatomy of modern forms has yielded indirect evidence of the evolutionary history of the group. Paleontological evidence seems also to indicate that the primate sequence was: tree-shew-like ancestors — to lemur-like — to tarsier-like — to cercopithecoid-like — to pongid-like and culminated (in the Pleistocene) in the hominids.

The book, according to the author, is "an introductory textbook which is intended for students of whom some may have no special knowledge of comparative anatomy." Because the author has made an effort carefully to explain and/or illustrate the anatomical structures which he discusses, the book could be used successfully as a "text" in an introductory Physical Anthropology course. To apply the term "textbook" to a publication, however, is usually to stigmatize it as far as the general reader is concerned. This I do not wish to do. I feel the general reader interested in his biological background will find the contents interesting and the author most articulate.—GEORGE R. BERNARD, Department of Gross Anatomy, Medical College of Georgia, Augusta, Georgia.

NOMENCLATURE OF PLANTS. By Harold St. John. Ronald Press, N.Y. 1958. 157 pp. $2.50.

When Henry Van Dyke wrote that "naming things is one of the oldest and simplest of human pastimes" he did not contemplate the International Code of Botanical Nomenclature. Professor St. John's little book is a kind of game book, designed for advanced botany classes where what he views as the fun of nomenclature is played. Honestly there are not likely to be many such games played around the world, if, indeed, there exist many advanced classes in plant taxonomy where the boards might be set up. When the cards are down most instructors in plant taxonomy would rather devote the precious few hours of their class to the handling of living plant materials, cherishing every moment for direct contact with the angiosperm creation in

all its varied forms. But there are always a few minds, as every teacher has discovered, who are fascinated by the application of essentially legal decisions to the names of organisms. The challenge is there but also the risk of excesses. It is unfortunate only when attention to nomenclature pushes aside the more important consideration of plant morphology, patterns of evolution, and the like.

The subtitle, "A Text for the application by the case method of the International Code of Botanical Nomenclature," sets the book's target. Chapter One explains the working of the Code and how it may be applied to a sample nomenclature case. Chapter Two contains all the principles encountered in the 1956 Code and, if there is time for one set of cases in the course of study, this chapter should be selected to demonstrate the rules in action. Chapter Three concerns the application of the rules to cryptogams; the remaining four chapters are lists of miscellaneous cases additional to those presented in the second chapter. Errors in typography are fortunately few, especially in view of the nature of the references. The interesting case of *Prosopis pubescens* Benth. in Hook., London Jour. Bot. 5:82. 1846 *versus* *Prosopis odorata* Torr. & Frem. in Fremont, Second Report 313 pl. 1. 1845, is an addendum that some instructors may find worth noting down on the blank pages provided at the back of this boundless subject. There was a decade in American botany when *nomen calare,* name calling, or the proper basis of nomenclature, moved over from the plant to the plantsman. Each succeeding International Botanical Congress moves a little closer to the Utopia when names, applied under a minimum of rules with a modicum of exceptions—officially "Nomina conservanda"—will serve their true function: linguistic handles of the utmost possible stability, applied in an imperfect world, for the communication among men of serious intentions concerned with the accurate recognition of organisms.—JOSEPH EWAN, Tulane University, New Orleans.

Books Received

CAVES OF ADVENTURE. Haroun Tazieff. Viking Press, Inc. 222 p., 16 illus. 1960. $1.45, U. S. $1.69, Canada.

ADVENTURING WITH BEEBE. William Beebe. Viking Press, Inc. 282 p., 15 illus. 1960. $1.25, U. S. $1.45, Canada.

MANUAL FOR OUTDOOR LABORATORIES: The Development and Use of Schoolgrounds as Outdoor Laboratories for Teaching Science and Conservation. Richard L. Weaver, Ed. Interstate Printers & Publishers, Inc. 81 p. 1959. $1.25.

LEAD POISONING AS A MORTALITY FACTOR IN WATERFOWL POPULATIONS. Frank C. Bellrose. Illinois Natural History Survey Bulletin. State of Illinois. 286 p. 1959.

RAINBOW TROUT IN MEXICO AND CALIFORNIA WITH NOTES ON THE CUTTHROAT SERIES. Paul R. Needham and Richard Gard. University of California Press. 108 p., 40 figs. and 8 plates. 1959. $2.50.

AN ECOLOGICAL ANALYSIS OF THE AVIFAUNA OF ST. LAWRENCE ISLAND ALASKA. Francis H. Fay and Tom J. Cade. University of California Press. 77 p., 3 figs. and 5 plates. 1959. $1.50.

TERTIARY STRATIGRAPHY OF THE BLAIRSDEN QUADRANGLE PLUMAS COUNTY, CALIFORNIA. Cordell Durrell. University of California Press. 31 p., 1 fig. 5 plates and 5 maps. 1959. $1.00.

THE LOVEJOY FORMATION OF NORTHERN CALIFORNIA. Cordell Durrell. Uni-

versity of California Press. 27 p., 1 plate and 4 maps. 1959. $1.00.

PLIOCENE AND LOWER PLEISTOCENE OF THE WESTERN PART OF THE SAN FRANCISCO PENINSULA. William Glen. University of California Press. 51 p., 5 figs., 2 plates. 1959. $1.00.

MANUAL OF COMPARATIVE ANATOMY. Bruce M. Harrison. C. V. Mosby Co. 352 p., and 122 drawings. 1959. $3.95.

MEET THE SOUTHWEST DESERTS. Philip Welles. Dale S. King, Publisher. Globe, Arizona. 82 p., numerous photographs. 1960. Paper, $1.00. Cloth, $2.25.

REPTILES: LIFE HISTORY, EVOLUTION AND STRUCTURE. Angus d'A. Bellairs. Harper Torchbook: The Science Library. Harper and Brothers, New York. 184 p. 1960. Paper, $1.35.

ANIMALS SPECIES AND THEIR EVOLUTION. A. J. Cain. Harper Torchbook: The Science Library. Harper and Brothers, New York. 183 p. 1960. Paper, $1.35.

PROBLEMS OF LIFE: AN EVALUATION OF MODERN BIOLOGICAL AND SCIENTIFIC THOUGHT. Ludwig von Bertalanffy. Harper Torchbook: The Science Library. Harper and Brothers, New York. 204 p. Paper, $1.35.

ANIMAL GROWTH AND DEVELOPMENT. Maurice Sussman. Foundations of Modern Biology series. Prentice-Hall, Inc., New York. 105 p. Illus. 1960. Paper, $1.50.

THE CELL. Carl P. Swanson. Foundations of Modern Biology Series. Prentice-Hall, Inc., New York. 103 p. Illus. 1960. Paper, $1.50.

AN ANALYSIS OF INTRASPECIFIC VARIATION IN THE KANGAROO RAT DIPODOMYS MERRIAMI. William Z. Lidicker, Jr. University of California Press, Berkeley and Los Angeles. Vol. 67(2), p. 125-218, plates 9-12, 20 figs. 1960. Paper, $2.00.

ECOLOGY OF THE PEREGRINE AND GYRFALCON POPULATIONS IN ALASKA. Tom J. Cade. University of California Press, Berkeley and Los Angeles. Vol. 63(3), p. 151-290, plates 17-26, 7 figs. 1960. Paper, $2.50.

HAWKS AND OWLS: POPULATION TRENDS FROM ILLINOIS CHRISTMAS COUNTS. Richard R. Graber and Jack S. Golden. Natural History Survey Division. Urbana, Illinois. 24 p. 1960.

WINTER FOODS OF THE BOBWHITE IN SOUTHERN ILLINOIS. Edward J. Larimer. Natural History Survey Division, Urbana, Illinois. 35 p. Illus. 1960.

A FIELD LIST OF BIRDS OF THE DETROIT-WINDSOR REGION. By Ralph A. O'Reilly, Jr., Neil T. Kelley and Alice H. Kelley. Cranbrook Institute of Science, Bloomfield Hills, Michigan. 40 p., 1 map. 1960. $0.50.